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ON FACTORS INFLUENCING THE GAS-EXCHANGE IN FISH

BY

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INTRODUCTION

Though the study of gas-exchange of all poikilotherm animals is attractive as being of great importance to the knowledge of metabolism in general, this holds still better for fishes, the only vertebrates which pass their whole life in water.

So it is clear, that there has been done a lot of research work as to the oxygen-consumption and carbondioxide-production by these animals under various conditions of temperature, O_2- and CO_2-pressure, pH, saltconcentration, etc.

The results of all these investigations are far from uniform and even often very contradictory. Now it is not an easy matter to measure the basal metabolism of mercurial animals like fishes, the more as the use of narcotics must be rejected, while their influence on life-processes always remains incalculable.

There have been made many attempts to eliminate the movements of fish by tying them up or by enclosure in narrow tubes, but it is clear that by doing so, the natural behaviour (and therefore respiration and metabolism) is already disturbed.

Moreover the method of measuring the gas-exchange consisted usually of analysis of the water in which the fish had lived. Thus it was impossible to measure the gas-exchange in a continuous way.

METHODS AND EXPERIMENTS

So we thought it desirable to study the gas-exchange in fishes using a more adequate technique. The animal is put into a glass vessel, which can be closed hermetically (except for an air in- and outlet) by means of a rubber disk and metal lid with pressing screws. There were three specimens of this vessel, the first containing 4 litres, a second one 2 and a small one for small fishes holding only 350 ccm.

An aircurrent, as a rule free from CO_2, is blown into the water through little filtering-stones which provide for a sufficient and regular ventilation. The outcoming gas, changed as to its O_2- and CO_2-contents by the animal, is analysed by means of a diaferometer developed by NOYONS. The gas-stream is kept constant and is controled by a rotameter. The fish behaves very quiet in this apparatus during the experiment.

Measuring the CO_2-output under basal conditions

The water in the vessel was freed from CO_2 by injecting CO_2-free air for a prolonged time before the fish was put in. The animal had been kept in the same room in order to preserve it from temperature changes, to which fishes seem to be very sensible.

WELLS (1935a) affirms, that the metabolic rate depends on the temperature at which the fish has lived before the experiment started. In our latter experiments we used to keep the animals day and night at constant temperature, which accorded to the constant temperature in the experimental vessel.

Our first experiments were carried out in order to acquire some knowledge as to the basal metabolism of fish in destilled water (a.d.). Fig. 1 shows the CO_2-output of a roach (*Leuciscus rutilus* L.) of 61 grams and of an ablet (*Alburnus alburnus* L.) of 28 grams. The amount of CO_2 produced per gram of body weight and per minute is plotted against time. It is evident, that only after several hours a constant minimum CO_2-production

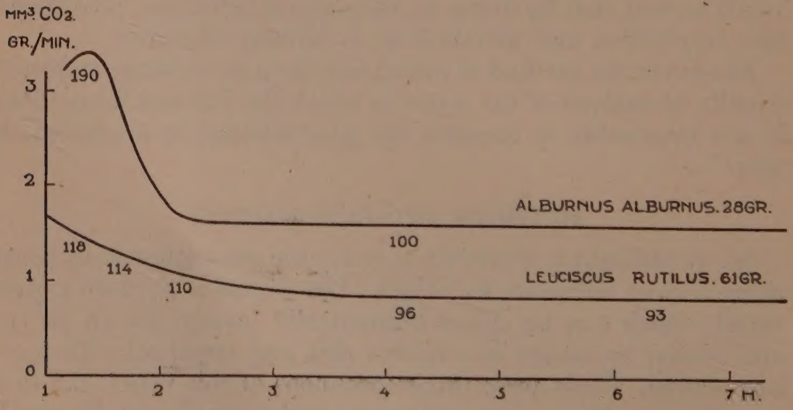

Fig. 1. Carbondioxide production in destilled water. Figures give frequency of respiration.

TABLE 1

Roach (*Leuciscus rutilus* L.); 17 cm long; 61 grms (in 4 litres aqua dest.)

No.	Temp.	CO_2-production in cmm per gram per min. after:						
		½ hour	1 hour	2 hours	3 hours	4 hours	5 hours	6 hours
5	19°2		1.95	1.58				
6	18°4			1.89				
7	17°8		1.59	1.40				
11	16°		1.38	1.21				
15	15°6			1.26				
16	15°8	1.80	1.59			0.79	0.76	
17	16°2			1.42			0.75	0.75
18	15°8			1.10			0.75	0.75
19	16°3		1.39	0.79	0.80			
23	17°	1.68	1.26		0.99	0.90	0.83	0.85
24	16°		1.28	0.96				
25	16°							0.83

is obtained. Table 1 shows the results of measurements of the CO_2-production of the same roach at different times during the experiment. The CO_2-production proves to be very constant, but only after a rather long time of experimentation, that is to say, it takes a long time before the fish becomes quite accustomed to the new situation.

That this is the right interpretation of the sloping down of the CO_2-line is also proved by the frequency of the respiration which runs parallel to it. Thus only after several hours the fish is accustomed to the milieu and we may assume that we are measuring the basal metabolism.

The destilled water will of course not keep its purity during the experiment, the fish spoiling it by excretions and production of mucus. But this cannot be the explanation for the sloping down of the CO_2-line; for a second experiment with the water already used a previous time shows the same results.

In the appreciation of described results of metabolism-experiments in fish one has to reckon with this peculiarity, especially in short-time experiments.

It was to be expected that the use of ordinary tap-water would show a different result at any case in the beginning of the experiment. Tapwater contains more or less alcali and this may hold part of the CO_2. Fig. 2 proves that this proposition is right. It shows the CO_2-output of one and the same roach in destilled

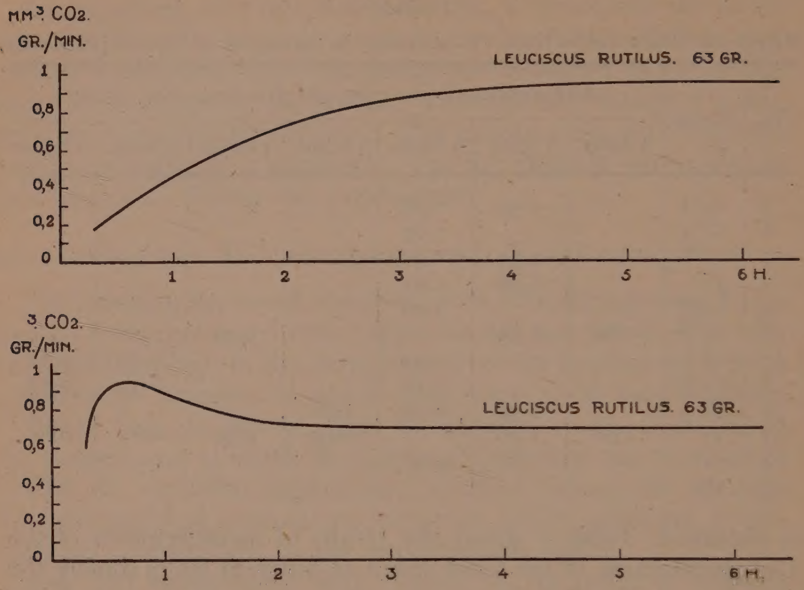

Fig. 2. CO_2-output of roach in tapwater (above) and in destilled water.

water and in tap-water; the latter graph only inclining slowly (the large vessel of 4 litres hold was used) owing to the binding power of the tap-water.

As the first part of the experiment, with the declining or inclining CO_2-line was not of any use to us, we always waited several hours before starting the measurement of gas-exchange.

Influence of temperature

There exists an extensive bibliography on the influence of the temperature on the rate of metabolism of fishes. LEINER (1938) gives a good summary. Several authors announce that the rate of the gas-exchange increases with rising temperature as a rectilinear relation. Other investigators claim to have found a more exponential curve, which was often taken in relation to the Van 't Hoff-Arrhenius' equation.

Table 1 (pag. 3) shows already some relation between rate of gas-exchange and temperature but we wanted to study this influence more in detail. Therefore we performed experiments, in which the temperature was raised step by step. On each tem-

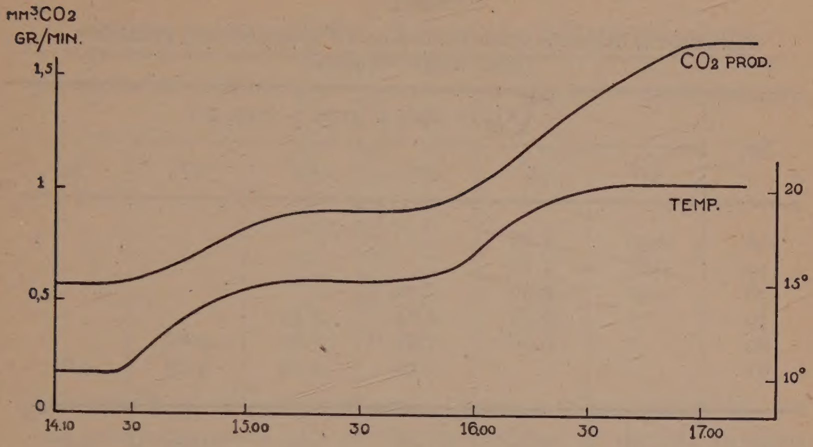

Fig. 3. Relation between water-temperature and CO_2-production; goldfish.

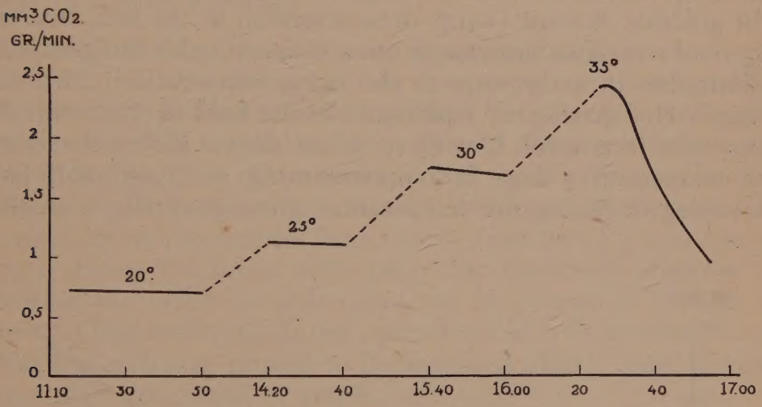

Fig. 4 CO_2-production at different temperatures; goldfish.

perature-level we waited until the CO_2-production had reached a constant value. This occurred with some retardation as to the temperature of the water (fig. 3). Only at high temperatures the CO_2-output falls down at prolonged duration of the experiment. Probably this is the result of an increasing injuring influence: at 35° C the animal dies. (fig. 4).

Table 2 and fig. 5 show the results of a series of experiments on goldfish (*Carassius auratus* L.). The temperature relationship to the metabolic rate is reflected as a curve, which shows a

TABLE 2

Influence of different temperatures on CO_2-output in 5 goldfishes (total weight 68 grms)

No.	CO_2 in cmm p. grm. p. min. at:					
	10°	15°	20°	25°	30°	35°
76	0.97	1.16				
77	0.81	1.18				
78	0.56	0.92	1.70			
79		0.93	1.64	2.45		
80		0.96	1.82	2.49	3.62	
81			1.56	2.04	3.29	4.62
M =	0.78	1.03	1.68	2.33	3.45	4.62

striking resemblance to the one, given by Ege and Krogh (1914) for goldfish. Krogh (1914) drew attention to the fact, that the Q 10 of metabolic processes is not a constant value but gradually diminishes in accordance to the rising temperature. Thus the Van 't Hoff-Arrhenius' equation does not hold to the metabolic processes in general. Our Q 10 values show a different relation to temperature: there is a maximum Q 10 at 15°–20°, both lowering or raising the temperature gives gradually a smaller

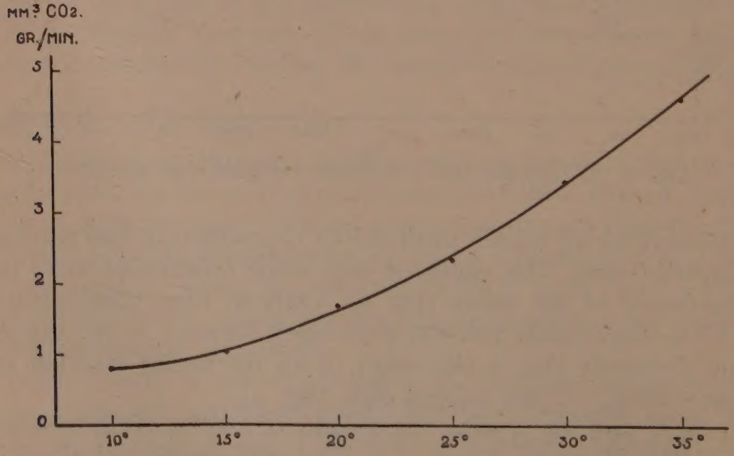

Fig. 5. Relation between temperature and CO_2-production in goldfish.

TABLE 3

CO_2-production in goldfish. Q 10 range at different temperatures

10° –15° C	1.85
12°5 –17°5 C	2.14
15° –20° C	2.34
17°5 –22°5 C	2.23
20° –25° C	2.16
22°5 –27°5 C	2.11
25° –30° C	2.03
27°5 –32°5 C	1.93
30° –35° C	1.85
32°5 –37°5 C	1.78

Q 10 (tab. 3). Whether this is a question of maximum Q 10 at the temperature of 15°–20° (being optimal to the life processes in this fish) will be a subject for further investigations.

Influence of feeding

The kind of food too is of great importance to the gas-exchange of the fish. This influence is best demonstrated in tab. 4 which shows the O_2-consumption of goldfish fed during a prolonged time with dried daphniae. According to KNAUTHE (1897) this chitin holding food exerts an important specific dynamic action, the metabolic rate is even to increase with 100%. To become sure about this we successively fed a tench (*Tinca tinca* L.) with bread, meat, bread and bread with chitin. The latter was prepared by boiling the dried daphniae-plancton in potassium hydrate of 10 %. Only chitin stands this operation and is to be washed out. The gas-exchange proved to be increased after a meal of meat and after the intake of chitin (tab. 5).

Perhaps the influence of feeding forms also an explanation for the well known phenomenon that the metabolic rate gradu-

TABLE 4

Influence of feeding on O_2-uptake in goldfish in tapwater at 20° C

No	O_2 in cmm p. gram p. min	diet
125	2.14	well fed on dried daphniae
127	1.59	after two days fasting
129	2.21	after 1 gm. dried daphniaes

TABLE 5

CO_2-production p. gram p. min. of tench 53 grm. at different diet. Temp. 20° C

No.	date	diet	CO_2/gr/min.
150	28/5	bread	0.814
151	29/5	bread	0.820
153	2/6	bread	0.836
154	3/6	bread	0.800
156	12/6	meat	1.02
157	16/6	meat (one week)	1.11
159	25/6	1 × bread	1.07
160	1/7	1 × chitin + bread	1.21
163	6/7	bread (5 days)	0.996
164	7/7	1 × chitin + bread	1.135
165	15/7	fasting (one week)	0.88

ally diminishes under laboratory circumstances. PÜTTER (1909) records this for seahorses (*Hippocampus*), and other fishes. In our investigations too this phenomenon was clear, especially in a series of experiments on *Rhodeus amarus* L. Table 6 gives a general view. According to the minute proportion of these fishes we always used 10 animals at a time; the medium being tapwater at pH 7, 8. The table shows the CO_2-output per gram of body weight per minute. The body-weight, decreases over the time of the experiments and also proves that the decrease in metabolism is obviously a matter of feeding.

TABLE 6

CO_2-production of Rhodeus amarus L. in tapwater at pH 7.8 Temp. 22° C

No.	Date 1942	medium weight grams	CO_2-output in cmm. p. grm. p. min.
92	6/2	2.20	4.33
94	11/2	1.85	4.20
95	11/2	1.93	4.03
96	13/2	1.63	3.28
97	14/2	1.93	3.90
98	16/2	1.63	4.35
99	17/2	1.63	3.89
100	18/2	1.93	3.43
101	20/2	1.61	3.15
117	14/3	1.35	1.84

The relation between metabolic rate and size in fish

In fish, just as in other animal beings the large specimen show a relatively smaller metabolic rate, than the small ones. (see Leiner, 1938). Our fig. 1 (page 2) shows already this phenomenon: the CO_2-production per gr. per min of the smaller ablet is much higher than that of the roach. Table 7 gives this relationship in more evident way, showing the CO_2-output in grams of body weight in roaches of different weight. The CO_2-rates have some spreading as the experiments were not carried out at one and the same temperature. moreover the temperature and so the rate of gasexchange was lower than the figures shown in table 1, but still in the mean values the correlation between body weight and rate of CO_2 production is evident. It is tried to explain this fact for homoiotherm animals in assuming that by the relatively smaller surface of the larger specimen the output of energy by radiation etc. would be relatively smaller too. If the gas-exchange of similar warmblooded animals of different sizes is calculated per unit of surface area the results thus obtained show pretty much about the same value. The same re-

TABLE 7

CO_2-production in roach of different sizes in cmm p. grm. p. min.

No.	Temp.	Weight in grams		
		16.3	30.3	60.5
38	14°	0.78		0.55
39	13°	0.75		0.56
40	13°	0.81		0.63
41	12°2		0.84	0.56
42	12°2	0.90	0.82	
43	13°6		0.93	
46	11°4		0.64	
47	12°2		0.76	
48	12°0			0.62
52	13°4		0.62	
M =		0.81	0.77	0.58
surface in cm^2		57.86	87.47	138.69
CO_2 in $cm/cm^2/min$:		0.228	0.267	0.253

sulted from our investigations. The numbers in table 7, which show the CO_2-production per unit of surface area in roach, are obtained by calculating the surface area from the body weight by means of the formule:

$$\text{surf. area} = k \times (\text{body weight})^{2/3}$$

For fishes k is equal to 9 (Rubner 1924).

The influence of pH

There are but few subjects so much discussed in literature as the relation between breathing in fish and the load of CO_2 and O_2 and the pH of the water. The large discrepancies in literature are due principally to the use of animals of various kinds which will react differently at this factor, according to the different tension of loading of their blood. As to the pH, Wiebe and collaborators (1934), H. Meyer (1935) and Hall (1931) adjudge great influence to this factor. A pH lower than 6.3 would be accompanied by a much decreased O_2-consumption, according to the latter two authors. We carried out experiments with *Rhodeus* and goldfish on the influence of pH on O_2-uptake at constant temperature of 22° C. A former investigation by us stated, that CO_2-output of *Rhodeus* in destilled water was considerably smaller than in tapwater (see table 9) a result which could not be obtained with other fishes (roach, tench, gold-

TABLE 8

Influence of pH on gasexchange in goldfish;
O_2 and CO_2 in cmm p. grm. p. min.

No.	milieu	pH	CO_2	O_2	R.Q.
102	tapwater	8 7.8	1.39	1.86	0.75
103	„	8 7.8	1.15	1.58	0.73
104	„	8 7.8	1.20	1.50	0.80
105	„	8 7.8	1.17	1.44	0.81
110	buf. 1/1000	8 7.5	1.14	1.39	0.82
106	„ 1/3000	7.6 7.3	1.24	1.69	0.73
113	„ 1/1500	6.8	0.95	1.31	0.70
107	„ 1/3000	6.4	1.16	1.36	0.85
108	„ 1/3000	5.6 6.7	0.96	1.25	0.76
109	„ 1/1000	5.6 6.4	1.30	1.37	0.95
111	„ 1/300	5.3 5.8	1.32	1.37	0.96
112	dest. water	6.2 6.8	1.07	1.43	0.75
114	buf. 1/1000	7.3	0.97	1.20	0.81

TABLE 9

Influence of pH on gasexchange in Rhodeus amarus

O_2 and CO_2 in cmm p. grm. p. min.

No.	Milieu	pH	CO_2	O_2	R.Q.
82	destilled w.	6.2	2.63		
83	”	”	2.52		
84	”	”	2.87		
85	”	”	2.44		
94	tapwater	7.8	4.20		
100	”	”	3.43		
101	”	”	3.15		
115	buf. 1/3000	6 6.4	2.21	2.62	0.84
116	buf. 1/3000	7.9 7.7	1.88	2.60	0.72

fish). Hall and Meyer point out that a declining pH goes parallel to a decreasing O_2-consumption and we thought this to be the explanation of the different behaviour of *Rhodeus* in destilled water. The latter namely has a considerably lower pH than the Utrecht tapwater. But this explanation cannot be right, for a series of experiments comprised in the table 8 and 9 does not approve this statement. These tables show the CO_2-output and O_2-uptake of *Rhodeus* and goldfish in different mediums as tapwater, destilled water and buffer-solutions. The buffer-solutions were made according to Sørensen, by using K-and Na-phosphates in destilled water, at concentrations which ran from 1/3000 up to 1/300 molair. The figures show no definite relation between pH and gas-exchange.

Possibly it is not the pH that is of great importance, but the salt-concentration. For in changing the pH one has to add or withdraw salt-ions to or from the water. We have to count with this circumstance in judging the experiments of other authors on this subject.

Another most interesting fact is, that we were not able to keep the pH at a constant value. Even in buffer concentrations up to 1/300 Mol. the pH proved to go towards the neutral point during the experiment; this is clearly shown in table 8. If the pH was 5.6 at the beginning of the experiment it rises to 6.7 (no. 108); from pH 8 it falls to 7.5 (no. 110). The rate of rising or falling depended on the concentration of buffersolution used. Whether this is due to the buffering power of the fishmucus or is caused by salt-ion uptake by the fish is not yet established.

Influence of CO_2-pressure

The experiments on the influence of CO_2-pressure on O_2-consumption in goldfish (table 10) do not show a clear result. The rates of gas-exchange are rather different from day to day. In general the uptake seems to be somewhat decreased at higher CO_2-pressure. Only at an amount of 9.5 % CO_2 in the injected airstream there was obviously a diminished O_2-uptake. Possibly the influence of CO_2-pressure is more important in other fishes.

TABLE 10

O_2-consumption of 4 goldfishes (total weight 65 grms) at 20° C at different CO_2-standards in the injected gas

No.	% CO_2	cmm O_2 p. grm. p. min.
112	0	1.438
104	0	1.47
105	0	1.44
118	0.03	1.13
119	1.18	0.87
122	2.34	1.23
120	4.60	1.28
123	5.99	0.93
121	7.99	1.45
124	9.49	0.74

Influence of O_2-pressure

Though a lot of investigators claim that O_2-pressure is very important as to the rate of gas-exchange (HALL 1929, LEINER, 1937) this is denied by others (AMBERSON 1924, GAARDER 1918, HENZE 1910, RAFFY 1931, WINTERSTEIN 1908). It may be granted that there is a close relationship between O_2-pressure and respiratory movements. However, different species of fish will not react to this influence in the same manner. This manner of reaction may on its turn influence the rate of O_2-consumption and CO_2-output and the fidget of the fish. The affirmation by some authors that increasing the hold of O_2 in the aquariumwater up to 100 % of total gas amount is followed by an intensification of O_2 uptake may to our opinion be explained by this fact.

If the stream of CO_2-free outdoor air which is injected in our experimental vessel is interrupted and replaced by a stream of pure oxygen, to the same amount per hour the fish (tench) does not react at all. The CO_2-output remains about the same (fig. 6B),

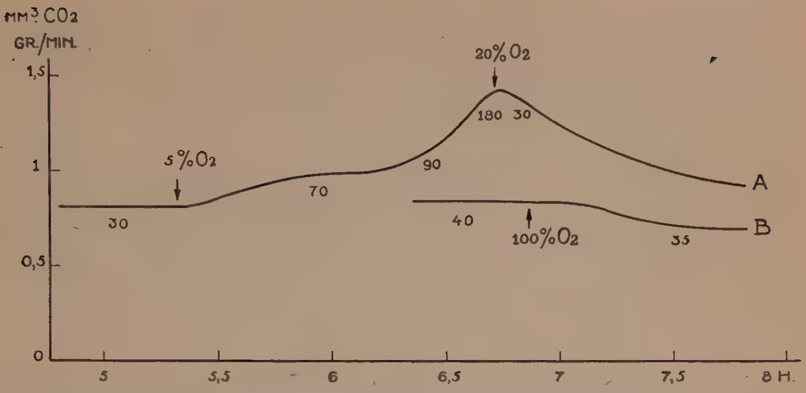

Fig. 6. CO_2-output at various O_2-pressures. Tench. 20° C.

perhaps a small decrease is to state. Only in goldfish there now and than was, as result of this change in gassupply, a certain transitory increase in CO_2-output. LEINER (1934) too announces an initial increase in O_2-consumption lasting over about half an hour after the exposure of seahorses to 100 % oxygen. But our experiments on goldfish were not reproducible and so they are of no importance.

If a gas-mixture was offered containing less than 20 % O_2, there always resulted an increased CO_2-output, except in one case of very low O_2-pressure (3 % of the total amount of gas) in goldfish, where it fell down; the animal evidently going to be

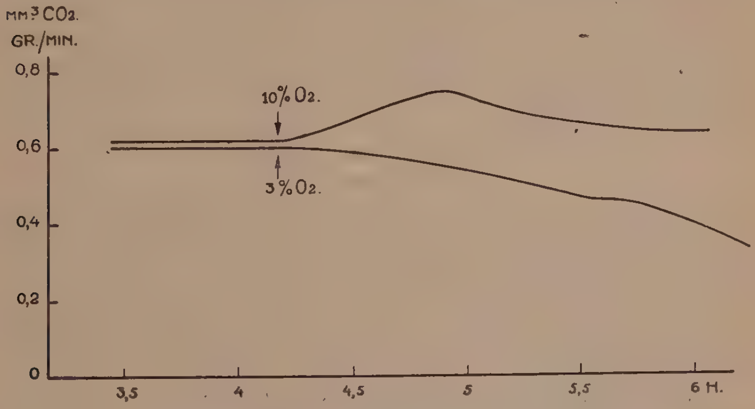

Fig. 7. CO_2-output at various O_2-pressures. Goldfish. 20° C.

paralysed (fig. 7). This augmentation in CO_2-production often was of transitory nature and was accompanied by a rise of the respiration-rate. It ceased at the moment of renewed injection of atmospheric air without CO_2 (fig. 6A).

Resuming we may conclude that one has to be very cautious as to the interpretation of experiments on the influence of gas-pressures on metabolism. One has to take into account the fact that low, and perhaps abnormal high oxygen-pressures too, may influence the respiratory-movements, but also the whole fidget of fish and as a consequence the (basal) metabolism.

Finally we carried out some experiments to estimate the influence of thyroxin on metabolism in fish. We started from the proposition that the uptake of thyroxin perhaps could be performed in fish through the gill-blades, the augmentation of metabolism then being an indication of the hold of thyroxin of the water. This would be a new and easy method to standardize thyroxine-preparations. Thus we injected thyroxin solutions into the experimental vessel, when the normal constant value of gas-exchange had been reached (*Rhodeus* and goldfish). Except for a transitory diminishing of the CO_2 reading probably caused by the alcalinity of the thyroxin solution, never any effect on gas-exchange was stated. So it is most evident, that thyroxin cannot pass through the gill membrane.

We also tried to determine the influence on metabolism of the application of progesteron to *Rhodeus*. It is known, that this hormon causes a prolongation of the oviduct of this little fish in some hours (see DUYVENÉ DE WIT 1938). The only result was now and then some inclination in the line of CO_2-output, but the curves were more or less irregular and so we cannot draw any definite conclusion.

SUMMARY

1. Using a new method in which fishes were kept in their natural circumstances the metabolic rate of these was established by means of the diaferometer-technique.

2. The relation between the size of fish and the rate of gas-exchange per unit of body weight could be affirmed. The surface-area-law is discussed.

3. The influence of temperature is studied; the Q 10 has probably a maximum value at optimum temperature.

4. The influence of CO_2- and O_2-pressure is discussed. Most fishes did not react at 100 % O_2; at lower pressures a higher metabolic rate may be found, due to increased fidget of the animals.

5. Salt concentration probably is more important than pH of the water as to metabolic rate of fishes.

6. No results were obtained as to the influence of thyroxin and progesteron, added to the water, on the metabolism of *Rhodeus amarus* L.

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CEREBRAL SKULL AND FACIAL SKULL

A CONTRIBUTION TO THE KNOWLEDGE OF SKULL-STRUCTURE

BY

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In a treatise on the skull which appeared in a Dutch handbook of the comparative anatomy of Vertebrata, I extended the distinction between cerebral and facial skull usual in human anatomy to lower Vertebrata (1941, pp. 245–249). In this article it is my intention to discuss and justify this extension.

The skull consists, as we shall see, of a number of comparatively separate functional parts, differing in size, position and grouping. This has made it possible for a facial skull and cerebral skull to be distinguished at a superficial examination.

Orbita, nasal cavity and upper-jaw will be regarded as the essentials among the most striking parts of the facial skull. If they form a coherent and separable complex in front of the cerebral skull, we may speak of a facial skull.

According to this formulation there can be no question of a distinction between cerebral and facial skull in the primitive platybasic skull. Here we have one single, wide cerebral cavity, containing the olfactory part of the brains as well, and continuing very far to the rostral part of the head. This applies to the Elasmobranchii, Dipnoi, Siluroidae and the Amphibia, possessing a primitive platybasic skull. In the Elasmobranchii the considerable rostrum protrudes before the cerebral cavity, but the rostrum gives no occasion to the formation of a facial skull. To this is added the fact that the upper-jaw of the Elasmobranchii is attached to the underside of the primordial neurocranium and does not protrude in the direction of the rostrum, because the rostrum protrudes over and in front of the mouth (*Heterodontus* and *Squatina* are excepted, see HOLMGRÈN & STENSIÖ, 1936, p. 319). In the Dipnoi, Siluroidae and Amphibia the cerebral cavity reaches to a relatively even greater distance in the rostral part of the head. The olfactory organ is only slightly developed in these groups, and does not much protrude. There is here, indeed, a new upper-jaw, situated outside and in front of the ethmoidal region of the skull, but this has no strong rostral development either. (In some primitive platybasic Stegocephalia and in some Hylinae only, a blunt snout has developed.)

But even if we wanted to limit the nasal cavity with the non-protruding new upper-jaw, and even if we wanted to limit the rostrum of the Elasmobranchii with the nasal cavities, not in any of these cases do the parts form a coherent combination with the orbitae, which, laterally directed as they are, are caudally situated at a clear distance. The fact that the cerebral cavity lies between the two orbitae and stretches further towards the rostral point, is connected with this. It is because of this that in the primitive platybasic skulls the orbitae cannot be separated together with rostrally situated parts from a caudally situated cerebral capsule.

So it is impossible to distinguish a cerebral and a facial skull in the primitive platybasic skull. In the tropidobasic skull this distinction is, in principle, very clearly marked, connected as we shall see, with the pushing back of the main mass of the brains to behind the orbitae and the septum interorbitale.

If, for these reasons on principle, we allow the distinction between cerebral skull and facial skull in tropidobasic skulls, and do not do so in primitive platybasic skulls, we must observe that in actual fact there are all sorts of transitions and difficulties. The distance between the inner walls of the orbitae – wide or narrow – is a relative thing. Also in the clearly tropidobasic skulls the hindmost cerebral cavity may have a more or less important rostral extension into the area of the septum interorbitale, and that generally dorsal. Neither is the distinction into tropidobasic and platybasic always very clear. Platybasism and tropidobasism may be dependent on the ontogenetic stage; *Amia*, *Lepidosteus*, Teleostei etc., start platybasic and take a tropidobasic line of development afterwards (HOLMGREN & STENSIÖ, 1936, p. 237). In primitive Stegocephalia, e.g. *Loxomma*, the skull is not clearly platybasic, but slightly tropidobasic (STADTMÜLLER, 1936, pp. 504, 508, 513). Also with regard to nasal capsule, orbita and upper-jaw, transitional conditions may be imagined.

Among the Amphibia the nasal capsules may extend in the rostral direction – combined with retraction of the brain – and even approach each other in the median line (STADTMÜLLER, 1936, p. 560, also 521).

The eyes, which in these lower groups are practically always laterally directed, have a partly frontal position in some Amphibia (NOBLE, 1931, p. 327).

The upper-jaw, or rather the snout or the secondary rostrum (see below) may considerably extend rostrally, also in primitive platybasic skulls.

But none of these tendencies as such, allow of a distinction between a facial and a cerebral skull in a primitive platybasic skull.

In the tropidobasic skulls a distinction between facial and cerebral skull is possible, because here the large orbitae, separated only by a septum interorbitale, form the boundary between a back part of the brain and a front part belonging to the facial part. Sometimes this division is dorsally accentuated; in those birds whose field of vision is principally directed upwards the cranial roof is dorsally narrow. This front – or facial part is accentuated by a rostral lengthening of the upper-jaw. This is possible because the new upper-jaw (praemaxillare and maxillare) formed by the dermatocranium, is not only situated in front of and outside the primitive upper-jaw but in the front and the extreme edge of the skull so that the mouth is terminally situated. At the same time dorsally situated elements have been lengthened, such as lacrimale, nasale etc. Generally the olfactory organ extends in the rostral direction namely by an extension of the olfactory epithelium, sometimes combined with the addition of a vestibular part. Without this rostral extension the opening for the nervus olfactorius would, after the reduction of the rostrum of the Elasmobranchii, be nearly situated at the rostral point of the skull.

In the secondary platybasic skull of the Ophidia, Amphisbaenidae, and Mammalia it is also possible to distinguish a cerebral and facial skull. In the Mammalia this is mainly due to the fact that the large, rounded, cerebral skull is clearly distinguishable from the differently formed snout. This snout consists of the rostrally elongated upper-jaw, generally connected with the rostrally elongated nasal capsule. The phenomenon of the secondary platybasity is connected with the development of such a snout. In the Mammalia the formation of such a snout is connected with the strong development of the jaws, in the Amphisbaenidae with their habitual boring. In the Ophidia we have to deal with another case: here the formation of a closed bony cerebral capsule as a defence of the brain in the swallowing of the very large prey is the primary reason of the platybasity.

In connection with this, the secondary platybasic skull forms one fixed whole, and cerebral and facial skull have been joined to one. In this case the orbitae do not, – as they do when a septum interorbitale is present –, separate two parts of the skull; on the contrary, the cerebral cavity runs between the orbitae, touching the nasal capsule between these orbitae. In the Mammalia the cerebral cavity penetrates generally only so far between the orbitae that they become or remain connected with caudally enlarged nasal capsules. The fact that the orbitae and nasal capsules are connected makes it possible for them to be, with the upper-jaw, regarded separately as one coherent whole: the facial skull. The cerebral cavity is no impediment to this distinction, because it only penetrates between the caudal parts of the orbitae and does not entirely separate them. In the Primates the situation of the orbitae in the facial skull is particularly accentuated. Whereas in the Mammalia the eyes are generally placed laterally, but to a lesser degree so than in Non-Mammalia, and at the same time are generally placed in the direction of movement, with horizontally placed eye-axis, we see in the Primates that the orbitae have been moved in a much more strongly rostral direction, and then have frontal position. The eyes may have a frontal position because the distance between the orbitae is small in connection with the reduction of the olfactory organ (STADTMÜLLER, 1936, pp. 883, 958, 990).

When, however, a distinction between cerebral and facial skull is possible, it is often not very clear.

This is the case where parts comparatively independent as to development of size and form, do not produce as it were secondarily the whole of the skull, but where the circumference of the whole is fixed and the component parts conform to this whole. In principle this may be expected in the streamlined heads of aquatic animals swimming in a special way, in several groups of fishes, Stegocephalia etc., and of animals burrowing in the earth. A streamlined head does, however, not in itself imply a streamlined skull. This is indeed the case in the teleostean fishes and the Stegocephalia, where the dermatocranium lies immediately below the epidermis. In teleostean fishes the tip of the bony secondary rostrum, immediately below the epidermis, serves as a bow or breakwater; this gradually passes into those parts of the skull situated behind, as far as the operculum, also immediately below the skin. The shape of the operculum is in its turn determined by the shape of the rostral part of the trunk and its transverse section etc. We may conclude that in teleostean fishes the whole shape of the skull is "sehr unter den Gestaltungsgesetzen des Gesamtkörpers" (MARINELLI, 1936, p. 229). In *Lepidosteus* the skull has been so much adapted to the demands of the very elongated shape, that even the brain has been deformed (MARINELLI, 1936, p. 228). The deeper lying primordial neurocranium is less influenced by the streamline principle than the superficial dermatocranium (MARINELLI, 1936, p. 229). The same is the case where the elements of the dermatocranium lie deeper, which occurs in secondary aquatic animals and in burrowing animals. All the same, there is also a certain influence on the deeper lying parts and thus the shape of the skull of water-mammals depends amongst others on the movement of swimming and other factors. According to certain opinions the consequences of the movement of the caudal fin of the Cetacea, and the influence of the water-pressure, on the asymmetry of the skull of the Cetacea, especially in the Odontoceti, and particularly in the facial skull, can be observed also in the chondrocranium, especially in the nasal skeleton (STADTMÜLLER, 1936, pp. 850, 905, 959, 987).

The distinction between a cerebral skull and a facial skull may be very clear – and sometimes is so – when it is not the circumference of the whole that is the determining factor, but when parts comparatively independent in the development of size and shape have developed separately and the circumference and shape are, as it were the secondary result. The most striking of these comparatively independent parts are the jaws – or rather the jaw apparatus with the masticatory muscles and their places of insertion – and in the higher developed ones (some Pterosauria, Theromorpha, Aves and Mammalia) also the brain (MARINELLI, 1936, p. 230; Versluys, 1936, pp. 706, 741). Speaking about the relation between facial skull and cerebral skull in the Mammalia STADTMÜLLER (1936, p. 956) says: "massgebend wirksam auf diese Relation" is "die Entwicklung des Gehirns und damit des Cerebralcraniums einerseits und die des Visceralcraniums mit dem Kauapparat andererseits". In the groups of Reptilia not mentioned above, where the brain is very small, it has no dominant influence on the skull and its external shape. It is obvious that the circumference of the skull as a whole is comparatively independent, and not determined by a streamlined whole in the land-animals with a clearly marked external neck, where the size of the head is independent of the section of the trunk.

The further determination of what elements of the skeleton – or, as we shall see later, parts of skeleton-elements – belong to the cerebral and the facial skull respectively, gives rise to all sorts of questions, difficulties and objections. These questions may, for the sake of clearness, be arranged into three groups:

1. What is the connection with the ontogenetic division into primordial neurocranium and splanchnocranium?
2. Is the plane of division between cerebral skull and facial skull situated on the outside surface of the skull or can it also be situated below the outside surface, i.e. in a space not occupied by skeleton-elements or connections of those?
3. Is the line of division or plane of division between cerebral and facial skull situated between not-fused skeleton-elements, or is it possible for this line or plane to run right through a perhaps complex piece of skeleton-element, or even between two intergrown skeleton-elements or even between the inner and outer blade of a skeleton-element?

Connection between the division of the skull into cerebral and facial skull, and the ontogenetic division into primordial neurocranium and splanchnocranium.

Under the influence of comparative anatomy and embryology it has evidently been tried in human anatomic circles to make a connection between the division of the adult skull into cerebral and facial skull and the division into primordial neurocranium and splanchnocranium, as is a.o. evident from remarks by Von Spee (1896, pp. 93, 95), Gaupp (1916, pp. 81, 83), Kopsch (1922, pp. 62, 132; 1940, pp. 186, 247) and Van den Broek (1922, p. 75; 1942, pp. 84, 116, 121). Max Weber (1927 I, p. 55) makes the same connection for Non-Mammalia. Here the cerebral skull is identified with pars neuralis, cranium neurale, neurocranium, cranium cerebrale, "Gehirnschädel" and "Schädelkapsel", and the facial skull is identified with pars visceralis, cranium viscerale, splanchnocranium, "Gesichtsschädel" and "Visceralskelett".

The science of comparative anatomy and embryology, especially of Non-Mammalia has in recent years led to the distinction of not two but three component parts of the skull, viz. the dermatocranium (MARINELLI, 1936, pp. 212/213) by the side of the primordial neurocranium (or neural endocranium) and the splanchnocranium (or visceral endo-skeleton) (HOLMGREN & STENSIÖ, 1936, p. 233). In a certain sense this marks a return to OWEN (1866 I, p. 26) who distinguished a "dermo-skeleton", "neuro-skeleton", and "splanchno-skeleton", and by the side of those a "sclero-skeleton".

We have seen that in cases where the dermatocranium is lacking, – presupposing that we have to deal with primitive conditions –, it is impossible to make the distinction: cerebral skull and facial skull. We must further observe that a sharp local division between neurocranium and visceral skeleton is not a matter of course; on the contrary, they primarily show a more or less wide, continuous connection, such as e.g. in the Cyclostomata and related primitive agnathic fossils (HOLMGREN & STENSIÖ, 1936, pp. 233, 238, 251, 262, 270, 271, 288, 294, 295). In the primitive Gnathostomata, neurocranium and visceral skeleton are primarily entirely unconnected, probably as a result of the more active ingestion which demands movable jaws (HOLMGREN & STENSIÖ, 1936, p. 233). Neurocranium and visceral skeleton are only secondarily connected in many Gnathostomata, the immovable attachment resulting from the fusion of the primitive upper-jaw with the neurocranium, only occurring where a widening of the pharynx is unimportant and where the food is chewed before it is swallowed (MARINELLI, 1936, p. 229).

Returning to the idea that the dermatocranium is a third equal component part of the skull, we must observe that the divergent characteristics of the elements belonging to the dermatocranium were known to human anatomists and embryologists. They thought, however, that these elements could be considered as belonging to either the cerebral skull, or the facial skull (GAUPP, 1916, p. 83; KOPSCH, 1922, pp. 62/63; 1940, p. 186; VAN DEN BROEK, 1922, p. 78; 1942, p. 87).

Though it may be possible to class the few remaining dermal bones on account of their close contact with the primordial human skull either with the primordial neurocranium or with the splanchnocranium, in the whole series of Vertebrata this is impossible. Then the dermatocranium appears to be a third, independent component. Here we shall only point out some facts connected with the subject of our paper.

Originally – except in fossil Cyclostomata (Holmgren & Stensiö, 1936, pp. 234, 239, 249) – the dermatocranium lies immediately below the epidermis and consequently the secondary cranial roof lies at a considerable distance of and entirely free from the completely separated and deeper lying primordial neurocranium, as is e.g. the case in Acipenseridae and largely also in *Neoceratodus*. The dermatocranium originates independent of the primordial skeleton, the secondary cranial roof originates at all events entirely independent of the neural endocranium.

For the rest the back-boundary of the dermatocranium, especially that of the secondary cranial roof, is independent of the back-boundary of the primordial neurocranium, which varies in length, as expressed by the old terms protometameristic and auximetameristic neocranium (Marinelli, 1936, pp. 211, 211/212).

Finally the kinetic skull in its most original shape, that of the metakinetic condition, teaches us that the skeletal covering of the brain consists of two separate parts: the bottom with the back part of the roof, and, apart from that, the much larger remainder of the cranial roof.

But also apart from these fundamental objections a deviation from the equalization of this ontogenetic division with that into cerebral and facial skull, would have been made. Thus Gaupp (1916, p. 81) says: "Wenn man . . . auch für den erwachsenen Menschenschädel an der Einteilung in eine Pars neuralis und eine Pars visceralis (Cranium neurale, Neurocranium, und Cranium viscerale, Splanchnocranium) festhalten will, so wird man jedenfalls dabei scharf betonen müssen, dass hier am ausgebildeten Schädel die Grenzen zwischen beiden Abschnitten etwas anders zu ziehen sind, als am embryonalen Schädel". Because the petrosum is situated in the wall of the brain-cavity, Gaupp (p. 81) proposes to include the rest of the os temporale, fused to one whole, in the cerebral skull. As "ein Kompromiss zwischen theoretischen und praktischen Gesichtspunkten" Gaupp (p. 82, also pp. 81, 83) then gives a subdivision in the form of a table from which it is evident that the cranium cerebrale consists of the pars neuralis or neurocranium without the cranium nasale or cranium praecerebrale. The latter consists of the ethmoidale with the conchae inferiores, the nasalia, lacrimalia and the vomer. Gaupp (p. 82) includes the ethmoidale in the cranium nasale "da es aus der Nasenkapsel hervorgeht", while it "zu dem cerebralen Schädel in viel weniger inniger Beziehung" is; "es ergänzt zwar vorn die Schädelbasis, aber nur in einem beschränkten Gebiete, und bei seiner Entfernung würde hier lediglich statt einer grösseren Anzahl kleiner Nervenlöcher ein grosses Foramen entstehen". – The cranium nasale mentioned above now forms, together with the cranium maxillare (consisting of maxillae, palatina, zygomatica and mandibula 1)) the cranium faciale. When we deduct this cranium cerebrale and the cranium faciale, only a few parts of the splanchnocranium remain, viz. the ossicula auditus and the os hyoides.

According to Gaupp (p. 83) the eyes with the orbitae lie "auf der Grenze des Cranium cerebrale und des Cranium nasale". As Gaupp includes a bone, also a complex bone, as a whole in one of the two parts of the skull, we may suppose that in the orbita the boundary between cerebral and facial skull runs, according to Gaupp, along a suture in the orbita. So, like Stratz (1904, p. 86) who says: "Als Grenze zwischen Gesichts- und Gehirnschädel nahm ich eine Linie an, welche vom unteren Rande des Stirnbeins ausgehend, über dem Jochbein zum Schläfenbein verläuft und den äusseren Gehörgang von oben umgreift". But in his turn, Stratz includes the processus zygomaticus squamosi in the cerebral skull, but the tympanicum in the facial skull.

Kopsch (1922, p. 62; 1940, p. 186) who identifies the cerebral skull with the neurocranium and the facial skull with the splanchnocranium, adds, however (1922, p. 63; 1940, p. 186 but without the second sentence): "An der Schädelkapsel im engeren Sinne, d.h. an der knöchernen Hülle des Gehirns haben keinen Anteil ein grosser Teil des Siebbeins, Nasenbein, Tränenbeine, die unteren Muscheln und das Pflugscharbein. In diesem Sinne hat man die genannten Knochen auch mit zu den Ossa faciei gerechnet". So here, too, we have a concession or compromise.

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1) Van den Broek (1922, p. 78; 1942, p. 87) takes this section from Gaupp with this alteration: he does not consider the mandibula to belong to the cranium maxillare and therefore not to the cranium faciale either. Von Spee (1896, p. 95), Spalteholz (1919, p. 36; 1939, p. 52) and Kopsch (1922, pp. 63, 105, 117, 135; 1940, pp. 186, 220, 229, 248) do consider the lower-jaw to belong to the facial skull.

Whether, and if so, in how far the orbitae belong to the facial skull, is not indicated.

According to Van den Broek (1922, pp. 75, 102, 104; 1942, pp. 84, 115, 121, see, however, p. 116) who, in outline, follows Gaupp, the orbitae are enclosed by the bones of the facial skull.

The opinion, cropping up here and there, that the orbitae are enclosed by the bones of the facial skull goes, without any doubt, back on earlier authors.

Thus Von Spee already (1896, pp. 93, 95) included not only the function of supporting the digestive tract but also that of supporting the sensory organs, in those of the facial skull; it is true that the internal ear is not meant, which, as a matter of fact, is situated within the os temporale which he includes in the cerebral skull; but maybe nasal capsule and orbita are included, although he includes the frontale as a whole in the cerebral skull.

And this idea of Von Spee's probably goes back on even older ideas, of which we mention Owen's (1866 I, pp. 26, 29, 103, 114) according to whom the "splanchno-skeleton" contains the bones connected with the sensory organs (including "petrosal" "sclerotal", and "turbinal") and with the viscera. Owen himself says (1866 I, p. 104) that if his four neural segments are only called "cranium" this "would exclude some bones called 'cranial' and include some called 'facial' in Human Anatomy". In my opinion sense capsules should be among those excluded "cranial" elements, although a further search after the meaning of the idea of sensory capsules is here certainly necessary (eye-capsule as over against orbita etc.).

If we do not want a compromise, but wish to identify the division between cerebral skull and facial skull with that into neurocranium and splanchnocranium, then, with Max Weber (1927 I, p. 80) we reach the conclusion that facial bones occur in the walls of the orbitae, and even more so in the nasal capsules.

We may draw the conclusion that the opinion prevails that the cerebral skull consists of the greater part of the primordial neurocranium (except the ethmoidal region and sometimes also the primordial orbita entirely or partly) and part of the so-called secondary cranial roof of the dermatocranium (except the operculum, the new upper-jaw, and the zygomatic arches).

Is the plane of division between cerebral skull and facial skull situated on the outside surface of the skull or can it also be situated below the outside surface, i.e. in a space not occupied by skeleton-elements or connections of those?

The cranial wall does not always and everywhere consist of one single skeletonous blade; in certain groups and in certain places two skeletonous walls lie at some distance from each other, and this space is not occupied by skeleton-elements or their connections. As an instance we mention the primordial cranial roof and the separate secondary cranial roof of Acipenseridae. What we are interested in in connection with our subject is the double wall – the lining of the cerebral cavity and the secondary cranial roof – in the area of the temporal region with the zygomatic arches, which walls are separated by the fossa temporalis. So the question is whether e.g. in *Chelone*, the cerebral skull is formed by everything situated behind the vertical plane through the hindmost ridge of the orbitae, or whether the outside wall, formed by the temporal region of the secondary cranial roof, belongs to the facial skull. In my opinion the latter is the case, and the cerebral skull is both laterally and dorsally almost completely surrounded by the temporal region of the secondary cranial roof, belonging to the facial skull, and hidden from view in a lateral and dorsal section.

The opinions regarding the condition in humans can scarcely be of great importance here as in man the temporal region of the secondary cranial roof has been reduced to one single zygomatic arch. For the sake of completeness we shall mention the opinions about the condition in humans. The os zygomaticum is generally considered to belong to the facial skull (Von Spee, 1896, p. 95; Stratz, 1904, p. 86; Gaupp, 1916, p. 83; Spalteholz, 1919, p. 34; 1939, p. 50; Kopsch, 1922, pp. 63, 135; 1940, pp. 186, 248; Van den Broek, 1922, p. 78; 1942, p. 87). As the maxillare belongs to the facial skull as well, this is certainly the case with the processus zygomaticus ossis maxillaris. The processus zygomaticus of the os temporale is certainly or almost certainly included in the cerebral skull by the above mentioned authors (see fig. Stratz, 1904).

Is the line of division or plane of division between cerebral and facial skull situated between not-fused skeleton-elements, or is it possible for this line or plane to run right through a perhaps complex piece of skeleton-element or between two intergrown skeleton-elements or even between the inner and outer blade of a skeleton–element?

In human anatomy the boundary between cerebral skull and facial skull is by some authors fixed along the sutures between the skeleton-elements. The line of division or plane of division between the two cranial parts lies then between not-fused skeleton-elements. I need here only point to Gaupp (1916, p. 81) who considers squamosum, tympanicum and processus styloides of the adult human skull as belonging to the cerebral skull "wie es bei ihrer Verwachsung mit dem Petrosum auch gar nicht anders möglich ist". In the same way the pterygoid, as part of the os sphenoidale is considered to belong to the cerebral skull (Gaupp, 1916, p. 83). Kopsch (1922, p. 63; 1940, p. 186) considers the lamina medialis processus pterygoidis in man as belonging to the facial skull.

The question now presents itself whether in other organisms where the component parts of human complex bones are still separate, (such as e.g. the os temporale and the os sphenoidale) the boundary between cerebral and facial skull must not be drawn differently. In my opinion a separate tympanicum and pterygoid will have to be considered as belonging to the facial skull, and not to the cerebral as in human beings. When the boundary between cerebral and facial skull is determined in accordance with specific fusion, so not on a comparative anatomic base, one ties oneself down to a fusion of the separate skeleton-elements and closure of the sutures which is specific for the group or species or race only. This fusion may take place during the embryonic and foetal existence, but also in youth, in adult and senile phases of life, during which many cranial sutures are obliterated. When the question is put on a comparative anatomic base, we must remember that in the most primitive groups the neural endocranium as well as the dermatocranium both form a sutureless whole (Holmgren & Stensiö, 1936, pp. 236/237, 239, 247/248, 249, 270, 303, 325, 344).

By the side of those authors who draw the boundary-line between cerebral and facial skull along the cranial sutures, there are also authors who, for certain bones, draw the boundary right through such a cranial bone.

This in itself, is not unnatural. In an entirely different domain we see a similar phenomenon: in the mesokinetic bird-skull we observe that the dorsal line of flexion between the occipital segment and the maxillary segment does not confine itself to the boundaries or sutures of the cranial elements.

Very artificial is the boundary between the neurocranium and the parts of the face, when an imaginary plane is constructed through AEBY's "Grundlinie des Kopfes"; by this many parts of the skull, such as orbita, ear-region, ethmoid, labyrinth etc. are cut in two (VON LUSCHKA, 1867, p. 16/17).

In the above we saw that KOPSCH (1922, p. 63; not in 1940) says that: "ein grosser Teil des Siebbeins" belongs to the parts considered as belonging to the ossa faciei, as this part of the ethmoid does not form part of the bony cover of the brain. SPALTEHOLZ (1919, p. 22; 1939, p. 38) says of the os ethmoides that it "bildet teilweise den unteren (kaudalen) Abschluss des Gehirnschädels in dessen vorderstem (ventralem) Abschnitte, reicht aber mit seiner Hauptmasse tief in den Gesichtsschädel hinab (hinein) und beteiligt sich an der Bildung der Nasen- und Augenhöhlen". (n.b. these two latter cavities lie, according to SPALTEHOLZ, 1919, pp. 59, 62; 1939, pp. 75, 78, in the facial skull.) So the boundary between facial skull and cerebral skull would run right through the os ethmoides. The same is the case with the os frontale according to those authors who consider the whole of the orbita to belong to the facial skull (FLOWER & LYDEKKER, 1891, pp. 35, 36; SPALTEHOLZ, 1919, p. 59; 1939, p. 75; VAN DEN BROEK, 1922, pp. 75, 102, 104; 1942, pp. 84, 115, 121, see however p. 116). In this connection we are also reminded of the human orbitosphenoidea and alae parvae ossis sphenoidei, which are situated in the wall of the cranial capsule as well as in that of the orbita.

A further difficulty is represented by the cases where two skeleton-elements have intergrown in such a way that the outer element does not form part of the lining of the cavity. Thus the nasale lies on the cartilaginous ethmoidal region and does not belong to the lining of the cerebral cavity.

With the squamosum, conditions become very intricate. In the lower Vertebrata, the squamosum is situated on the outside, against the cerebral skull. In the higher Vertebrata the squamosum may be situated in the lining of the cerebral cavity; this is connected with the enlargement of the cerebral capsule in consequence of the enlargement of the brain (Aves, Mammalia) (Gaupp, 1916, p. 78). That, judged from the outward surface, the squamosum lies in the wall of the cerebral skull does not necessarily imply that it lies on the inside surface of the cerebral cavity; in Mammalia the ala pterotica may partly or entirely cover the inside of the squamosum. In nearly all Aves and most Mammalia the squamosum does indeed lie in the inner lining of the cerebral capsule (Owen, 1866 2, pp. 313, 425; Kingsley, 1925, pp. 136, 181; Marinelli, 1936, p. 819).

The parietale may be excluded from the wall of the cerebral capsule as occurs in Odontoceti (Kingsley, 1925, p. 211), but this is highly exceptional.

By the side of the phenomenon of a skeleton-element being superimposed as a whole on one (or more) skeleton-element(s), and therefore being excluded from forming part of the lining of the cavity situated below, and the other phenomenon that skeleton-elements are situated side by side in a plane, the phenomenon occurs that skeleton-elements cover each other in part, because they have slipped across each other, and lie imbricately. Where is in such cases the plane of division between facial skull and cerebral skull?

Yet different difficulties present themselves in the division between facial skull and cerebral skull when the cerebral cavity is surrounded by extremely thick walls, so that such a wall cannot simply be considered as a covering of the cerebral cavity.

Also a wall of the cerebral cavity which is in the main thin may be thick in parts, e.g. in the region of the internal ear. This region is, however, generally considered to belong to the cerebral skull.

Sometimes, however, the entire wall of the cerebral cavity is very thick. In some cases this thickness is solid, as e.g. in a number of marine Vertebrata (Stadtmüller, 1936, p. 958); and in certain Dinocephalia this solid wall is extremely thick (Versluys, 1936, p. 707). This is the phenomenon of the pachyostosis, hyperostosis or osteosklerosis.

In most cases this thick wall is, however, spongy or pneumatic. The latter is exceptional in Reptilia and only occurs in Crocodilia and perhaps in Pterosauria; it is very common in Aves, and also occurs fairly often in Mammalia. Spongy bone also often occurs in Aves and Mammalia. Whether a thick wall of the cerebral cavity consists of solid bone, spongy bone or is pneumatic in the Mammalia depends on the size of the skull and whether it occurs in a water- or a land-animal. [1] In general the pneumaticity of the skull is, in the Mammalia, proportional to the size of the animal, at all events in land-animals; it reaches its maximum in the skulls of giraffes and elephants and also in *Rhinoceros*. Big water-mammals have on the contrary no or slightly developed pneumaticity (WEBER, 1927 I, pp. 53, 93). A big skull with moreover strongly developed ridges, edges and other surface enlargements is very heavy if it consists exclusively of solid bone. This great weight offers no difficulties to water-mammals because of the upward pressure of the water. In those few land-mammals which do have a very large skull, it would certainly be a drawback if it were very heavy. The weight is here reduced by the occurrence of spongy or pneumatic bone. Through this large junctures for muscles are possible without a too great increase of the weight of the skull.

When these junctures are situated on the outside surface of the wall of the cerebral capsule, separated from the real lining of the cerebral cavity by a thick layer of spongy or pneumatic bone, it will be clearly indicated that we have to deal with two separate functional elements of the skull: one juncture for muscles and one lining of the cerebral cavity. This is accentuated morphologically: the pneumatic or spongy bone-mass is namely on both sides covered by solid bone, forming the surface. This is the outer surface and the surface of the inner cavity. We may also state it in this way: the outer covering and the inner lining do not coincide, but there is a space in between which, in this case, is either spongy or pneumatic. Such conditions give rise to the opinion that the skull is a collection of functional elements (such as cerebral capsule, ear-capsule, nasal capsule, orbita etc.) of which the covering walls need not coincide but leave some space in between that may be filled with solid bone, but also with pneumatic or spongy bone. Considered in such a way a wall of the cerebral capsule is, on the inside a lining of the cerebral cavity and on the outside a juncture for neck-muscles, masticatory muscles etc., for which ridges, edges and other enlargements of the surface may serve as well.

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[1] This is, of course, apart from the primary function of pneumaticity, such as e.g. the function of tympanal pneumaticity as a resonance apparatus, and as a means to isolate sound-waves.

Stadtmüller (1936, p. 947) in his treatise on the skull of mammals formulates it like this: "Bei den statischen Beanspruchungen der verschiedenen Schädelabschnitte und der Sonderbeanspruchung der einzelnen Schädelknochen durch Muskelansätze kommt es oft zu einer Diskrepanz und damit zur Ausbildung funktionell nicht beanspruchter Hohlräume wie auch in anderen Skelettabschnitten, hinzu tritt beim Schädel noch als ausschlaggebend seine Zusammensetzung aus morphologisch und funktionell ganz ungleichwertigen Komponenten (Gehirnkapsel, Augentrichter, Nasentunnel, Zahnplatte, Gehörkapsel), deren Wände – das ist das Wichtigste – nicht zusammenfallen, sondern zwischen sich Zwischenräume lassen, die architektonisch tote Räume sind, aus ihnen werden die Pneumatizitäten". According to Stadtmüller (pp. 947/948) spongy spaces may occur instead of pneumatic ones. In his discussion of the Amblypoda this author (p. 956) includes – contrary to the above mentioned opinion – the outside boneridges in the cerebral skull.

We are, however, of opinion that, however important the distinction between facial and cerebral skull may be, more important still is the consideration of the skull as a combination of a great number of comparatively separate functional units.

As such functional units we mention: 1. cerebral capsule. 2. skeletal labyrinth. 3. orbita. 4. nasal capsule. 5. upper-jaw, upper-bill and snout. 6. lower-jaw. 7. suspension mechanism of the upper-jaw. 8. suspension mechanism of the lower-jaw (maxillary-joint). 9. juncture of the masticatory muscles to the "cerebral skull". 10. juncture of neck- and trunkmuscles. 11. juncture of other head-muscles. 12. foramen magnum. 13. condyli occipitales. 14. ear-ossicles. 15. skeletal frame of the tympanic membrane and the skeletal cover of the middle ear and external auditory meatus. 16. foramen pineale. 17. circumorbitalia and sclerotic ring. 18. foramen or fenestra antorbitalis. 19. paired spiraculum in the secondary cranial roof. 20. skeletal closure of the external nostril. 21. juncture and plane for horns, antlers etc. 22. collar. 23. cavity for glands. 24. toothplate. 25. palate. 26. axis-function of the parasphenoid. 27. lipskeleton. 28. gill-skeleton. 29. pharyngeal bone. 30. suspension of the shoulder-girdle. 31. pericard-capsule and cardiobranchiale. 32. operculum. 33. tonguebone-skeleton. 34. laryngeal skeleton. 35. cartilago epiglottica. 36. trachea.

Undoubtedly this enumeration is not exhaustive. I do not mean the numerous openings for nerves, blood-vessels etc. In my opinion they do not form a functional element. Some doubt, it is true, may be entertained about the fossa endolymphacea of Elasmobranchii and about the cranial bones which, in the lower Vertebrata with a superficial dermal armour support the slime- or sensory channels. On the other hand it is possible that this division has been pushed too far. It is certainly not quite accurate to consider upper- and lower-jaw as separate functional units. For practical reasons this has been done all the same.

A number of these functional units is indeed entirely separate, such as e.g. the lower-jaw, the ear-ossicles, the elements of the gill-arches, the radii branchiostegi, the trachea etc. Sometimes it depends on the group whether a component part is separate or fused. We discussed this already for the splanchnocranium with regard to the neurocranium in primitive agnathes as opposed to primitive Gnathostomata. Further we mention here the anulus tympanicus in mammals.

The question presents itself how it may be explained that the cranial parts mentioned, although they are separate functional units, are yet, as a rule, united into one whole. The answer must be sought in the fact that this is the condition for the fulfilment of certain functions demanded of the skeleton of the head.

We mention here: the preservation of the shape of the head, a demand that is in a very special way covered by the skull of recent larval Cyclostomata, with their continuous, superficially situated box of mucous cartilage (Holmgren & Stensiö, 1936, p. 275 ff.), by the continuous, sutureless endocranium of cartilaginous fishes and Branchiosauridae, and finally in many fossil fishes from the groups of the Cyclostomata, Placodermata and primitive Teleostomi, by the endocranium and in the Cephalaspids by the dermatocranium both forming a sutureless, bony whole. The next general function is that of the defence of the head by the superficial dermatocranium, which serves as an armour. Then the skull is the passive apparatus of movement of the head with regard to the neck. Thus also, the main mass of the skull is the passive apparatus of movement of the lower-jaw with regard to that remaining main mass of the skull. Sometimes this function is filled by the greater part of the neurocranium, with regard to the movable primitive upper-jaw. Also, in land-animals as opposed to water-animals, the weight of the head is very important, it demands great firmness of the skull (VERSLUYS, 1936, p. 717).

On the ground of functional demands of certain small parts we can sometimes conclude that they have to be united with adjacent parts to one larger coherent whole. When the rostral part of the skull serves as a bow, it may be understood that in teleostean fishes the so-called secondary rostrum must be firmly attached to the more caudally situated parts of the skull, and that, if this hindmost part of the skull does not form one whole, as is e.g. the case in tropidobasity and movability of the upper-jaw in Teleostomi, the parasphenoid acts as a connecting and consolidating axis (MARINELLI, 1936, p. 229). In the secondary water-animals of the higher classes of the Vertebrata, that "bore" their way through the water, we find a firm, coherent skull too. Here we meet with akinesis, i.e. the primitive upper-jaw forms a fixed whole with the primordial neurocranium. In burrowing animals, a firm, coherent skull is also a matter of necessity. Thus we often find much bone in the boring and burrowing Gymnophiona, Amphisbaenidae etc. In the Gymnophiona the connection between the enlarged elements remaining after the reduction, may be an adaptation to the boring habits. When the upper-jaw is well-developed and bears a strong tooth-plate, it will necessarily be attached to a firm skull with which it forms one fixed whole. For this are needed special pillars, constructed and situated according to mechanic demands. A strongly developed lower-jaw demands a strong connection between its point of articulation and the rest of the skull. The strong connection between the sensory capsules and the cerebral capsule may perhaps be explained by the fact that brain and sensory organs are situated on and against each other, and the necessary defence of the acting nerve. We will not silently pass by the fact that a morphological independence of the sensory capsules is supposed to exist (MARINELLI, 1936, p. 218). The attachment of masticatory and neck-muscles, – to mention a couple of strong muscle-groups –, demands that the juncture of such a muscle should be firmly attached to the other parts of the skull. The same holds good for the attachment of horns and antlers. It is generally supposed that the distribution of the compact parts, of spongy and pneumatic bone in the skull is adapted to the functional mechanic demands of pressure and pull and tension in the attachment of the muscles, the carrying of protuberances like antlers etc., the firmness of the skull as a whole, etc.

The importance of the union of the component parts of the skull to one whole, may be further proved from the skull of the birds. Each of the three main parts of the bird-skull (cerebral capsule, upper-bill and lower-bill) consists of a fused, sutureless combination. This is connected with the great firmness required, which is assured by this, the thin walls of the skull and their pneumaticity notwithstanding. (The light built of the skull is connected with the capacity for flying and the long neck, and the latter is again connected with walking on the hindlegs.)

Thus we have come to know a number of causes for the union of functional units to larger combinations. Before discussing a number of recurring combinations we shall first point to the reverse phenomenon, viz. that lower functional units are sometimes divided into two. In the metakinetic skull the cerebral capsule belongs partly to the occipital, and partly to the maxillary segment; the cerebral capsule consists of two separate pieces. In the Crossopterygii the endocranium falls into two parts situated one behind the other, separated according to a transverse plane, running through the back part of the opening for the nervus trigeminus (Holmgren & Stensiö, 1936, p. 347). In the Acipenseridae the dermatocranium, which in higher forms takes part in the formation of the cerebral capsule, lies separate, and at a clear distance from the primordial neurocranium.

So, although the skull consists of a number of comparatively independent elements, we see certain combinations of those elements occur. Thus we see the wall of the cerebral capsule habitually combine with the skeletal labyrinth in the "cerebral skull". In the same way we see the combination of upper-jaw with nasal capsule and orbita in the "facial skull". This combination is understandable because the upper-jaw as well as the olfactory organ develop, in accordance with their function, in the rostral part of the skull, and thus go together. Through the situation of the nervus opticus with regard to the nervus olfactorius, the orbitae may lie in the vicinity of the nasal capsules; in the tropidobasic and secondary platybasic skulls they form together one coherent whole.

In the "cerebral skull" as well as in the "facial skull" functional components have been united to a higher morphologic whole.

By the side of those, there are also combinations of a higher functional unit. I mention upper- and lower-jaw with their joint, and the juncture of the masticatory muscles. There is a functional connection between the juncture of the neck-muscles and the situation of the foramen magnum.

In a certain coherent combination of functional elements, united to a higher morphological whole, the mutual situation of the elements is determined by a number of factors, such as their relative size, but also by their shape. Here the fact that functional units need not be strictly homologous in different animals, which may result in difference of size or shape or situation, may play a part. As regards the shape of the functional units it must be observed that different units do not show similar characters. By the side of organs, occurring in the trunk of the body, that have a typical shape of their own, such as heart, testis, air-bladder etc. other organs occur bearing clear traces of having been influenced in their shape by adjoining organs, such as e.g. lung, milt etc., while yet other organs make the impression of conforming to the remaining space and so have hardly a specific shape at all, such as e.g. in fishes, the pancreas, liver and kidney. In the skull we also meet with these three types, with all their gradual transitions. Thus, according to STADTMÜLLER (1936, p. 947) orbita and nasal capsule are: "Organen mit Eigenraum" for which the strong "Verstrebungen" between certain parts of the skull, especially between the parts bearing the teeth, and the cerebral capsule, must make room, "was zu Umgehungskonstruktionen führt". According to MARINELLI (1936, p. 810) the mesokinesis of the bird-skull must be regarded as "ein Nebenerfolg der infolge der Gehirn- und Augenvergrösserung eintretenden Verschiebungen im Vogelschädel". According to STRESEMANN (1927–1934, p. 5, see also p. 48) the enormous increase in size of the eyes of the birds has led "zu einer weitgehenden Umgestaltung des Schädels: Verkleinerung der Schläfengrube unter Verdrängung der dort entspringenden Muskeln in okzipitaler Richtung, Verkürzung des vorderen Schädelabschnittes, Komprimierung der Orbitosphenoidalia bis zur gegenseitigen Berührung im Septum interorbitale, Aufrichtung der Hirnachse", while also "die Ethmoidalia von der Schädelkapsel völlig abgedrängt

(sind)" and "(zu einer) Deformierung der ursprünglich schön gerundeten Hirnkapsel führen kann". By the side of orbita and nasal capsule I should like to include in those parts of the skull that have "Eigenraum": skeletal labyrinth and laryngeal skeleton. As cranial parts that in part clearly conform to their surroundings – think of the streamlined skulls – I mention cerebral capsule (often more spacious than the brain, which as a matter of fact may conform to the streamline), gill-skeleton and operculum. Skull-elements without a specific shape of their own do not really occur, unless we want to regard the pneumatic and spongy bones as such. STADTMÜLLER (1936, p. 948) speaks in this connection of "passivity".[1]

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ELEKTROPHYSIOLOGIE DES PERIPHEREN NERVENSYSTEMS [1])

VON

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Die Forscher, die sich mit Untersuchungen über die Funktion des tierischen Organismus beschäftigen, haben bereits vor vielen Jahren entdeckt, dass die Energie, welche der Organismus aus der Nahrung gewinnt, sich zum Teil als elektrische Energie kund gibt. Man hat nämlich festgestellt, dass an nahezu allen biologischen Phasengrenzen Potentialgefälle auftreten, manchmal sogar relativ sehr grosse. Solche Potentialsprünge treten z.B. auf zwischen dem Protoplasma der lebenden Zelle und ihrer Umgebung, zwischen Zellkern und Plasma, u.s.w. Später, als die fortschreitende Entwicklung der physikalischen Technik tiefergehende Untersuchungen ermöglichte, stellte sich alsbald heraus, dass zwei Organsysteme existieren, bei denen diese Potentiale eine besonders wichtige Rolle spielen, und zwar beim Muskel- und beim Nervensystem. Beschränken wir uns auf das Nervensystem.

Eine Nervenzelle besitzt eine Anzahl von Fortsetzungen, von denen die Axone (Neurite, Nervenfasern) meistens nur einige μ dick sind und sehr lang werden können. Während die Zellkörper (Perikarya) grösstenteils im Zentralnervensystem angehäuft sind, treten die Axone aus den Zentren hinaus und vereinigen sich mit Axonen anderer Zellen zu Bündeln (Nerven). Bekanntlich haben diese Nerven eine charakteristische Funktion. Einerseits verbinden sie unsere Sinnesorgane mit dem Zentralnervensystem und übermitteln als solche die von den Sinnesorganen perzipierten Reizen nach den Zentren. Andererseits bilden die Nerven die Glieder zwischen Zentren und Effektoren; sie werden daher z.B. auch Impulse vom Zentralnervensystem nach den Muskeln überbringen, damit diese sich kontrahieren.

Man hat nachweisen können, dass das Potentialgefälle, welches zwischen Innen- und Aussenseite der Nervenfaser besteht, für das Überbringen dieser Signale von grundlegender Bedeutung ist. Dass, ebenso wie an anderen biologischen Phasengrenzen, auch an der Grenzschicht der lebenden Nervenfaser ein Potentialsprung vorliegt, wurde schon vor ungefähr einem Jahrhundert von Du Bois-Reymond entdeckt. Wir können diesen Potentialsprung am Nerven auf einfache Weise messen, (s. Abb. 1A), indem wir einen Nerven aus dem lebenden Organismus herausschneiden, auf die unverletzte Aussenseite eine Platinelektrode bringen und auf die Schnittfläche eine zweite, ähnliche Elektrode. Verbinden wir diese beiden Elektroden mit einem empfindlichen Galvanometer, so zeigt der Galvanometer einen Spannungsunterschied an, der in günstigen Fällen etwa 100 mV betragen kann. In anderen Fällen (abhängig von der

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[1]) Nach einem Vortrage, gehalten auf der Versammlung der Ned. Stichting voor Biophysica am 6-6-1942.

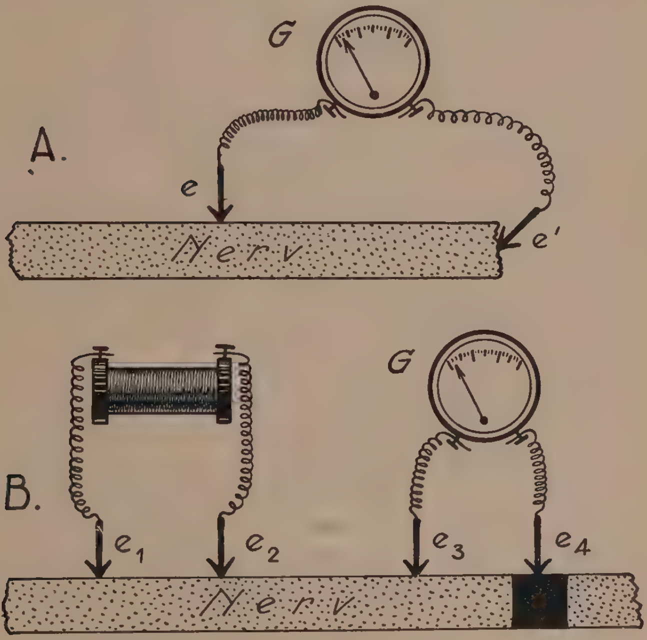

Abb. 1: A. Schema der Ruhestrommessung am Nerven. e und e^1 Ableitungselektroden.

B. Schema der Versuchsanordnung zur Reizung des Nerven und zur Registrierung der monophasischen Aktionswelle. e_1 und e_2 Reizelektroden, welche mit einem Induktionsapparat verbunden sind. e_3 und e_4 Ableitungselektroden; der Nerv ist unter e_4 abgetötet (schwarz).

Tierart und von dem gewählten Nerven) ist der Potentialsprung viel kleiner, manchmal nur einige mV. Dieser Spannungsunterschied gibt selbstverständlich, wenn Aussen- und Innenseite des Nerven über einem Galvanometer kurz geschlossen sind, Veranlassung zum Fliessen eines Stromes. Dieser sogenannte Ruhe-, Verletzungs- oder Demarkationsstrom bleibt unter günstigen Umständen stundenlange fliessen. Dabei geht aus der Stromrichtung hervor, dass die Aussenseite der Nervenfaser immer positiv und die Innenseite immer negativ geladen ist.

Fragen wir uns ab, was wohl die Ursache dieses Potentialsprunges an der Grenzschicht der Nervenfaser sein kann, so besteht an erster Stelle die Möglichkeit, dass ein Diffusionspotential vorliegt. Es sollte in diesem Falle fortwährend ein Stoff aus dem Nerven heraus diffundieren, der dissoziiert ist in grossen trägen Anionen und kleinen schnellen Kationen. Die kleinen Kationen diffundieren schneller, eilen sozusagen immer etwas voran, wodurch ein gewisser Potentialsprung auftreten kann. Diffusionspotentiale sind aber, wie man nachgewiesen hat, unter den Umständen, welche im lebenden Organismus herrschen, nie grösser als etwa 10 mV und sie sind demnach zu klein zur Erklärung der tatsächlich vorliegenden Spannungsdifferenzen. Etwas weiter kommen wir schon, wenn wir annehmen, dass die Nervenfaser umgeben ist durch eine selektiv permeabele Membran, welche durchlässig ist für kleine Kationen und undurchlässig für grosse Anionen. Die Anionenbewegung wird auf diese Weise ganz gehemmt, während die Kationen, welche eine gewisse Bewegungsfreiheit innerhalb der Attraktionssphäre des Anions besitzen, sich zwischen Innen- und Aussenseite der Membran bewegen können. An der Aussenseite der Membran entsteht somit eine gewisse Positivität und an der Innenseite selbstverständlich eine gewisse Negativität (Membranpotential).

Die Ansicht, dass sich um die Nervenfaser herum eine selektiv permeabele Struktur befindet, wurde schon von Bernstein (2) vertreten und hat auch experimentelle Bestätigung erfahren. Bis vor kurzem wusste man jedoch nicht, welche Ionen bei diesem Membranpotential eine Rolle spielen. Bear und Schmitt (3) haben neuerdings nachweisen können, dass im Plasma der Nervenfaser eine sehr grosse Menge von Kaliumionen angehäuft ist, und zwar ungefähr 18 mal soviel als im umgebenden Blut. Diese Kaliumionen werden im Nervenplasma wahrscheinlich durch grosse organische Anionen (vielleicht

Aminosäuren) in Gleichgewicht gehalten, weil die vorhandenen kleinen anorganischen Anionen (Cl, HCO_3, usw.) dazu nicht ausreichen. Die Kaliumionen sind die kleinsten Kationen, die im System vorkommen; sie können, wie experimentell gezeigt wurde, durch die Membran permeieren, die grossen Anionen dagegen nicht. Die Bedingungen für das Entstehen eines Membranpotentials sind demnach im Nerven völlig gegeben.

Hill (12) hat jedoch berechnet, dass der Potentialsprung am Nerven viel grösser ist als beim Vorhandensein eines reinen Membranpotentials unter diesen Umständen möglich wäre. Es scheint somit doch noch etwas anderes, etwas mehr vorzuliegen als einem physikalisch-chemischen Gleichgewicht entsprechen würde. Das ist aus neueren Experimenten deutlich hervorgegangen. Manche Untersucher, z.B. Cowan (8), haben nämlich nachweisen können, dass die elektrische Ladung der Nervenfaser sehr labil ist und nur erhalten werden kann durch ständigen Sauerstoffverbrauch, also durch fortwährende Oxydationsprozesse im Nervenplasma. Nimmt die Sauerstoffspannung im Milieu ab oder bringen wir den Nerven in eine Stickstoffatmosphäre, so wird die Ladung kleiner; nach erneuter Sauerstoffzufuhr erholt sie sich wieder. Lund (14) und Marsh (15) zeigten auch bei anderen lebenden Zellen, dass ihre Phasengrenzpotentiale dem Sauerstoffverbrauch direkt proportional sind. An der Grenzschicht der Nervenfaser herrscht also offenbar ein stationärer Zustand, der energetisch auf einem höheren Niveau liegt als bei einem rein physikalisch-chemischen Gleichgewicht möglich wäre. Dieser, durch fortwährende Energiezufuhr aufrecht erhaltene elektrisch stationäre Zustand ist von ausschlaggebender Bedeutung für die Übertragung von Signalen durch den Nerven.

Was nun eigentlich bei dieser Signalübertragung vorgeht, ist Gegenstand vielfältiger Untersuchungen gewesen. Festgestellt wurde, dass der, aus der Umgebung durch das Sinnesorgan aufgenommene Reiz sich als eine kleine, negative elektrische Welle durch die Nervenfaser fortpflanzt. Diese negative Welle nennt man den Aktionsstrom des Nerven; wir können ihn messen, indem wir zwei Elektroden auf dem Nerven anbringen und diese mit einem Galvanometer verbinden (Abb. 1 B). Man beobachtet dann, wie der Galvanometer nach Reizung des betreffenden Sinnesorganes einen zweiphasigen Ausschlag zeigt, da bei der Fortpflanzung des Aktionsstromes durch den Nerven zuerst die vordere Elektrode negativ wird hinsichtlich der zweiten und darauf die zweite Elektrode negativ wird hinsichtlich der ersten (zweiphasischer Aktionsstrom). Die Registrierung einer zweiphasigen Aktionswelle ist nicht immer erwünscht, denn der Aktionsstrom ist meistens so breit, dass die zweite Elektrode bereits negativ wird, bevor der erste zur Ruhe wiedergekehrt ist. In diesen Fällen erhält man ein verzerrtes Bild. Will man das vermeiden, so kann man das Gewebe unter der zweiten Elektrode abtöten; der Aktionsstrom pflanzt sich nämlich nur im lebenden Gewebe fort und erlischt demnach an der Grenze zwischen lebendem und totem Gewebe. Der Registrationsapparat schreibt bei dieser Anordnung nur eine einzige Welle, da nur die erste Elektrode negativ wird hinsichtlich der zweiten; die zweite bleibt in Ruhe (monophasischer Aktionsstrom). Die Dauer dieses Aktionsstroms (also die Zeit, in der die Welle unter einer Elektrode durchzieht) liegt in der Grössenordnung von einigen msec, bei schnellen Axonen 0.5–1, bei langsamen 10 und mehr msec. Die Spannung beträgt eine Anzahl von mV, sie schwankt zwischen ungefähr 0.1 mV und 100 mV, je nach der Tierart und dem Nerv, mit welchen experimentiert wird.

Es leuchtet ein, dass man für das Aufzeichnen dieser elektrischen Phänomene nicht nur eine äusserst empfindliche, sondern zugleich eine sehr schnelle, ohne Trägheit arbeitende Apparatur braucht. Das einzige Instrument, welches diesen Forderungen entspricht, ist der Kathodenstrahloszillograph, wenn man dabei einen Verstärker benutzt, welcher bis etwa millionenfach verstärken kann. Exakte Messung der Nervenaktionsströme ist daher erst möglich geworden, nachdem GASSER und ERLANGER (9) in 1922 den Kathodenstrahloszillographen in die physiologische Methodik einführten.

Beispiele von Aktionsströmen einzelner Nervenfasern, aufgenommen mit einem Kathodenstrahloszillographen, bringt Abb. 2.

Die Geschwindigkeit, mit welcher der Aktionsstrom sich über den Nerven fortpflanzt, kann stark schwanken; sie beträgt nämlich bei den schnellsten Fasern etwa 80 m/sec und bei den langsamsten weniger als 1 cm/sec. Dabei muss man im Auge behalten, dass der Aktionsstrom selbstverständlich nicht nur an der Oberseite der Faser läuft, sondern ganz um die Faser herum; die Welle pflanzt sich wie ein Ring um den Axon fort. (Abb. 3). Dieser Ring ist breiter, als man sich öfters vorstellt.

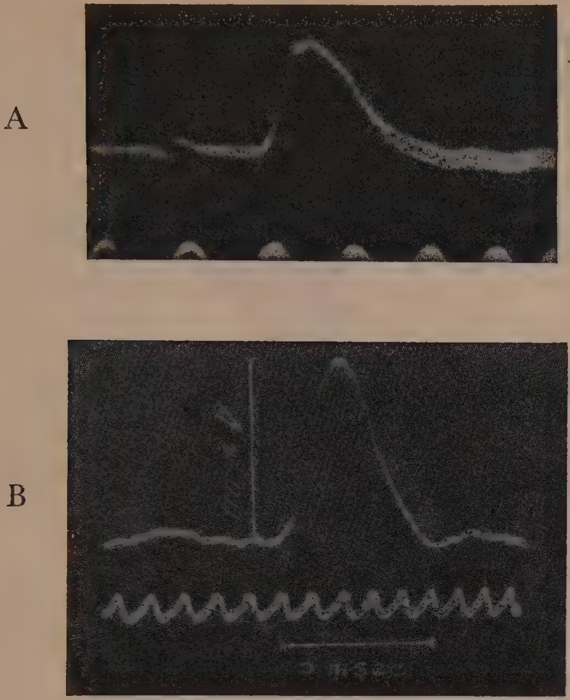

Abb. 2: Aktionsströme einzelner Nervenfasern. A: Von einem Katzennerven nach Gasser. Zeitmarkierung 5000 Hz. B: Vom N. pallialis von *Helix pomatia.* Zeitmarkierung 1000 Hz. Beide Aufnahmen mit dem Kathodenstrahloszillographen.

Stellen wir nämlich die Länge der durch die Aktionswelle gleichzeitig erregte Nervenstrecke gleich λ, seine Fortpflanzungsgeschwindigkeit gleich v und ist t die Zeit, welche der Aktionsstrom braucht um an einem Punkt des Nerven vorüber zu ziehen, so geht aus der Formel $\lambda = v.t$ hervor, dass bei v gleich 80 m/sec und t gleich 2 m/sec, λ 16 cm beträgt. Das heisst also, dass immer eine bedeutende Länge der Nervenfaser gleichzeitig aktiviert ist. Die Aktionswelle ist ein breites Band, vergleichbar mit einem Eilzug, der trotz seiner Länge doch in äusserst kurzer Zeit vorbeifährt, da seine Geschwindigkeit gross ist. Ist die Nervenfaser kurz (manche Fasern sind nur einige cm lang), so ist die Möglichkeit gegeben, dass die ganze Faser zur gleichen Zeit aktiviert ist.

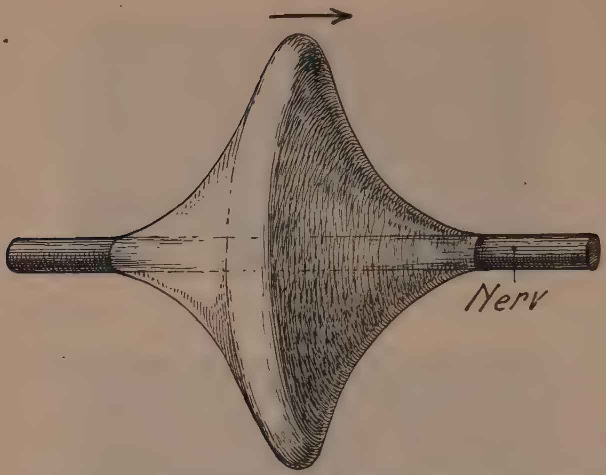

Abb. 3: Schema der Ausbildung der Aktionswelle, dargestellt als elektronegativer Ring um die Nervenfaser.

So weit einige Eigenschaften der Aktionswelle. Fragen wir uns nun, wie diese Aktion entsteht, so müssen wir den Zusammenhang betrachten, welcher zwischen Aktionsstrom und Ruheladung besteht. Einsicht in diesen Zusammenhang wurde erzielt durch jahrelange Versuche mit künstlicher elektrischer Reizung an isolierten Nerven in zahlreichen physiologischen Laboratorien der Welt. Erteilen wir dem Nerven einen elektrischen Stromstoss, so entsteht ein Aktionsstrom und zwar immer an der Kathode des Reizstromes (Versuchsanordnung s. Abb. 1B). Dieser Aktionsstrom pflanzt sich auf normale Weise fort und ist der auf natürliche Weise entstandenen Aktionswelle vollkommen ähnlich. Dieser künstliche Aktionsstrom ist an der Reizkathode entstanden; an dieser Stelle muss demnach die Ursache für sein Entstehen zu finden sein. Was geschieht an dieser Reizkathode? Daselbst ist durch den Reizstrom Negativität entstanden (Positivität vernichtet). Wenn diese Negativierung keine weitere Konsequenzen hätte, so müsste ein Gleichgewicht auftreten, das erhalten bliebe so lange der Reizstrom dauert. Es müssten in diesen Falle unter der Kathode positive Teilchen verschwinden, in einem Punkte daneben etwas weniger, daneben noch weniger usw. Auf diese Weise würde sozusagen ein negativer Hügel um der Kathode herum auftreten; an einer genügend weit entfernten Stelle des

Nerven würde man jedoch keine Potentialänderung beobachten. Da wir aber im Gegenteil sehr deutlich eine solche Potentialschwankung feststellen können (der Aktionsstrom, welcher sich fortpflanzt) so kann an der Kathode kein Gleichgewicht entstanden sein; der Reiz muss da selbst tiefer einschneidende Prozesse ausgelöst haben. Der Reizstrom hat nämlich an der Kathode die Grenzschicht durchlässig gemacht für die grossen negativen Anionen, die im Nervenplasma vorhanden sind, wodurch an der Reizstelle eine völlige Neutralisierung aufgetreten ist. Durch diese Neutralisierung werden auch nahe gelegen Punkte (Ringe) durchlässig, wodurch immer weiter entfernte Punkte der Membran durchlässig werden. Die Ruheladung wird somit an allen Punkten des Nerven nacheinander neutralisiert. Der mit den Ableitungs-elektroden verbundene Galvanometer zeigt bei diesem Vorgang selbstverständlich einen negativen Ausschlag (Aktionsstrom) an; die positive Ruheladung wird neutralisiert, sie verschwindet, die Aussenseite wird also negativ im Verhältnis zu den ruhenden Teilen.

Vorstehende Betrachtungsweise enthält einige Annahmen, welche wir näher begründen müssen. An erster Stelle wollen wir uns fragen, welche Gründe man für die Annahme des Durchlässigwerdens der Membran hat. Wird die Membran durchlässig für grosse Anionen, so muss der Ohmsche Widerstand stark abnehmen. Das ist tatsächlich der Fall. Verschiedene Forscher stellten fest, dass der Widerstand des arbeitenden Nerven abnimmt, und Cole und Curtis (7) haben in einem bestimmten Fall sogar messen können, dass der Membranwiderstand, der im ruhenden Nerven etwa 1000 Ohm/cm betrug, beim Durchziehen einer Aktionswelle herabsinkt bis zu 25 Ohm/cm. Daraus kann geschlossen werden, dass die Grenzmembran der Nervenfaser während des Passierens der Aktionswelle durchlässig wird für Anionen.

Ein zweiter unaufgeklärter Punkt ist, welche “Membran” der Nervenfaser man eigentlich als bei den elektrischen Prozessen wirksame Struktur betrachten muss. Man spricht allgemein über eine hypothetische Membran; die meisten Autoren geben aber nicht näher an, welche Membran nun eigentlich gemeint wird. Bei höheren Tieren hat man die Wahl zwischen verschiedenen Membranen. Um das Faserprotoplasma herum liegt hier erstens eine Markscheide, welche sehr lipoidreich ist, hierum eine dünne Zellschicht (Schwannsche Scheide), um welche manchmal noch wieder Bindegewebsschichten liegen. Bei niederen Tieren fehlt die Schwannsche Scheide vollkommen; die Markscheide ist da selbst sehr dünn und oft sehr arm an Lipoiden. Alle Nervenfasern aller Tiere haben jedoch eine morphologische Eigenschaft gemein: den Besitz einer dickeren oder dünneren Markscheide, mit mehr oder weniger Lipoiden. Diese Membran muss also bei den elektrischen Reizübertragungsprozessen eine wesentliche Rolle spielen.

Eine, und zwar die wichtigste, Frage muss jetzt noch beantwortet werden: Warum macht der Reizstrom an der Kathode die Grenzmembran durchlässig für grosse Anionen? Auf diese Frage geben viele Forscher eine unerwartete Antwort; so sind z.B. GILDEMEISTER (10), RUSHTON (19), BLAIR und ERLANGER (4) der Meinung, dass der Nerv ein Kondensator ist, welcher durch den Reizstrom aufgeladen wird; ist die Spannung genügend gross, so schlägt die Membran durch wie das Dielektrikum eines zu stark aufgeladenen Kondensators. Es ist jedoch sonderbar, dass man hier von einer Aufladung redet, denn an der Reizkathode, wo der Aktionsstrom entsteht, wird an der Aussenseite der Faser Positivität vernichtet. Es tritt also keine Erhöhung des Potentialsprunges zwischen Innen- und Aussenseite auf, sondern eine Erniedrigung. Keine Polarisierung, sondern Depolarisierung; keine Aufladung, sondern eine Entladung. Die Auffassung der genannten Autoren kann demnach nicht richtig sein.

Man hat bis jetzt nur ausnahmsweise daran gedacht (und dann meistens noch ohne die richtigen Folgerungen zu ziehen), dass bei der ruhenden Nervenfaser zwischen Innen- und Aussenseite der Membran ein sehr starkes Kraftfeld vorhanden ist. Setzt man z.B. den Potentialsprung auf 50 mV und den Durchmesser der Membran auf 100 Å (etwa die Dicke von 2 Lipoidmolekülen), so herrscht eine Feldstärke von 50000 V[1]). Im starken Kraftfeld, das in der Grenzschicht der Nervenfaser herrscht, werden polar gebaute Moleküle der Membran sich sehr wahrscheinlich nach den Kraftlinien ordnen. Dafür sind verschiedene Gründe anzuführen: ALCOCK (1) hat z.B. beobachtet, dass in einem Kraftfelde von 1000 V die Viskosität einer Lösung mit polaren Molekülen sich hochgradig ändert. SEIFRIZ (21) stellte fest, dass Protoplasmateilchen in einem elektrischen Felde sich durch ihre Polarität zu parallelen Fasern anordnen. Auch in der Nervenmembran selbst hat man mit Hilfe der Röntgenanalyse solche Orientierung beobachtet: BOEHM (5), UMRATH (23), HAUSSER (11) sowie SCHMITT und BEAR (20) sind der Meinung, dass die Lipoidmoleküle in der Nervenmembran radiär orientiert sind; die polaren Fadenmoleküle richten sich tatsächlich nach den Kraftlinien und ordnen sich gegenseitig auf gleichgrossen Abstand von einander an. Durch diese Anordnung wird die selektive Permeabilität der ruhenden Nervenfaser verständlich. Alle Teilchen, grösser als die Spalten zwischen den Fadenmolekülen (also die grossen Anionen im Nervenplasma) können nicht hindurch gehen; kleinere (Kationen) permeieren dahingegen.

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[1]) Man könnte der Meinung sein, dass die Membran bei dieser grossen Spannung durchschlagen müsste. Das ist aber nicht richtig, denn THIESSEN (zit. bei TRURNIT 22) hat nachgewiesen, dass monomolekulare Stearatfilme einen Potentialsprung von 5000000 V/cm ertragen.

Bringen wir nun eine Reizkathode auf den Nerven, so tritt an der Aussenseite der Membran eine gewisse Entladung auf (die Ladung der äusseren Kondensatorplatte wird vermindert); das Kraftfeld zwischen Innen- und Aussenseite wird also abgeschwächt, die straffe Anordnung der Membranmoleküle nimmt ab und die intermolekularen Kräfte kommen dadurch in die Lage, wirksam zu werden. Die Moleküle ballen sich demzufolge in unregelmässiger Weise zusammen, es tritt eine Art von Koagulierung auf. Auch das wurde festgestellt: OGGIONI (16, 17, 18) beobachtete, dass bei dem arbeitenden Nerven Granulationen in der Markscheide entstehen; die Röntgenanalyse hat gezeigt, dass während der Reizung Störungen in dem radiären Bau der Membran auftreten. Durch die gegenseitige Anziehung und die dadurch hervorgerufene Koagulierung der Membranmoleküle geht die Palissadenstruktur teilweise verloren; es entstehen grössere Löcher in der Membran, die grossen Anionen treten heraus, wodurch elektrisch eine vollständige Neutralisierung auftritt. Wenn aber an der Reizkathode Neutralisierung auftritt (die Ladung somit innen und aussen gleich Null wird), so werden Kationen und Anionen aus der Nachbarschaft angezogen, wodurch auch an diesen nahegelegenen Stellen das Kraftfeld abgeschwächt und somit auch die Membran permeabel wird. Dadurch tritt auch an dieser Stelle Neutralisierung auf, was wiederum Ionen von weiter entfernten Stellen anzieht, usw. Das Resultat ist schliesslich, dass die Membran nacheinander an allen Punkten permeabel und neutralisiert wird, was den Eindruck macht, dass eine negative Welle sich über die Nervenfaser fortpflanzt. Tatsächlich existieren nur Kreisströmchen, in Übereinstimmung mit der bekannten Theorie von HERMANN.

Ist diese Auffassung über das Entstehen des Aktionsstroms richtig, so werden an der Reizanode Prozesse im entgegengesetzen Sinne vor sich gehen müssen. Daselbst wird durch den Reizstrom die Positivität an der Aussenseite erhöht; das Kraftfeld wird hier somit stärker und die Membran neigt demnach weniger zu erhöhter Permeabilität. Das ist tatsächlich der Fall, wie experimentell auf viele Weisen festgestellt werden kann: An der Anode entsteht z.B. niemals ein Aktionsstrom und es ist dort eine besonders starke Negativierung notwendig, grösser als normal, um einen Aktionsstrom zu erwecken.

Aus dem Vorstehenden kann auch geschlossen werden, dass der sogen. künstliche elektrische Reiz gar nicht künstlich ist, sondern vollkommen adäquat. Der Aktionsstrom ist nämlich seinerseits wieder ein elektrischer Reiz für den nächstliegenden Punkt der Nervenmembran usw. Sowohl der künstliche Reiz als der Aktionsstrom sind von elektrischer Natur und auch von derselben Grössenordnung. Der natürliche Reiz (der Aktionsstrom) beträgt einige mV, und man hat nachgewiesen, dass unter günstigen Umständen der künstliche Reiz auch nur eine Spannung von einigen mV zu haben braucht, um Erfolg zu haben. Qualität und Quantität von künstlichem elektrischem Reiz und natürlichem Reiz sind also gleich; man kann daher den Nerven mit elektrischen Reizen stundenlang ohne Ermüdung oder Schädigung arbeiten lassen. Selbstverständlich braucht der Reiz nicht unbedingt elektrisch zu sein; im allgemeinen wird jedes Agens, welches imstande ist die Nervenmembran lokal genügend zu depolarisieren, als Reiz wirken und eine Erregung erzeugen. Die charakteristische Membranstruktur verschwindet dabei immer in demjenigen Augenblick, in dem die elektrische Doppelschicht vernichtet wird.

Will man dieses Membransystem mit seiner Ladung einen Kondensator nennen, so ist nichts dagegen einzuwenden, wenn man nur im Auge behält, dass hier kein Kondensator im gewöhnlichen Sinne vorliegt, bei welchem die Ladung erhalten bleibt durch die konstanten Eigenschaften des Dielektrikums, sondern vielmehr ein Dieelektrikum, welches bestehen bleibt, solange die Ladung konstant bleibt. Wird die Ladung verringert, so wird das Dielektrikum zerstört.

Das Sinnesorgan wirkt wahrscheinlich auf ähnlicher Weise wie der elektrische Reiz; es transformiert die aufgefangene mechanische, chemische oder Strahlungsenergie in elektrische Energie, welche das Nervenende depolarisiert, wodurch ein Aktionsstrom entsteht, der sich nach dem Zentralnervensystem hin fortpflanzt.

In Vorstehenden wurde wiederholt betont, dass der Aktionsstrom identisch ist mit Neutralisierung einer elektrischen Doppelschicht. Mehr als Neutralisierung kann hierbei selbstverständlich nicht statt finden, d.h. der Aktionsstrom eines bestimmten Nerven ist bei konstanten Bedingungen immer gleich gross. Das war schon lange bekannt; der arbeitende Nerv gibt immer alles was er geben kann; es entsteht immer ein Aktionsstrom von gleicher Grösse, gleichgültig ob schwach oder stark gereizt wird, vorausgesetzt, dass der Reiz nicht unterschwellig ist. Denn wenn man den Nerven zu schwach reizt, dann werden an der Reizkathode nur wenige positive Ionen vernichtet, zu wenig um das Kraftfeld genügend abzuschwächen zur Vernichtung der Membranstruktur. Das heisst also, dass eine bestimmte Reizstärke notwendig ist um die Schwelle überschreiten zu können. Der Begriff "Schwelle" ist in der Literatur nicht gerade klar; manchmal wird offen zugestanden, dass man nicht weiss was man darunter verstehen soll und andere Autoren haben komplizierte Differentialgleichungen aufgestellt, ohne jedoch dem Begriff "Schwelle" einen Schritt näher zu kommen. Dennoch scheint es mir möglich, eine Definition der Schwelle zu geben. Die Schwelle ist nämlich ein Potential, und zwar das kritische negative Potential, welches notwendig ist um die Nervenfaser so weit zu depolarisieren, dass die spezifische Struktur der Grenzmembran vernichtet wird. Wird die Faser zu wenig depolarisiert, so bleibt die Membran intakt und es geschieht nichts. Gibt man genügend, so fällt die Membran auseinander und es tritt Neutralisierung auf, also alles. Das ist das bekannte und viel umstrittene Alles-oder-Nichts Gesetz des Nerven, ein Gesetz, das in diesem Zusammenhang als eine logische Konsequenz der physikalisch-chemischen Konstellation der Nervenfaser hervortritt.

Wir werden nun zum Schluss noch eine Frage aufwerfen, und zwar diese: Ist der Aktionsstrom das eigentliche Signal, das durch den Nerv übertragen wird, der eigentliche Funktionsträger, oder nur eine Begleiterscheinung eines anderen wesentlichen aber unbekannten Prozesses, wobei ein Teil der freigemachten Energie als Elektrizität verloren geht? Struktur und elektrische Verhältnisse der Nervenfaser sind dermassen charakteristisch, dass man schon ohne weiteres dazu geneigt wäre, auf eine primäre Bedeutung des elektrischen Anteils der Nervenaktion zu schliessen. Dennoch sind manche Untersucher der Meinung, das elektrische Phänomen sei nur ein Nebenprodukt. BROEMSER (6) z.B. hat die Ansicht vertreten, dass der grundlegende Prozess der Reizübertragung ein Diffusionsprozess ist, welcher sich über den Nerven fortpflanzt; andere sind der Meinung, dass ein chemischer Prozess sich über den Nerven ausbreitet und als Nebenprodukt Elektrizität liefert. HILL (12) betonte aber schon nach Berechnung der bei der Aktionswelle frei werdenden Energie, dass die Existenz eines chemischen Prozesses äusserst unwahrscheinlich sei und HODGKIN (13) hat neuerdings endgültig bewiesen, dass das elektrische Phänomen primär ist. Er stellte Versuche an mit Riesenaxonen von Tintenfischen, die unter normalen Umständen eine bestimmte Leitungsgeschwindigkeit zeigten. Brachte er nun in der Ableitungsstrecke (also in der Strecke zwischen der zweiten Reiz- und der ersten Ableitungselektrode) eine Metallbrücke an, so pflanzte sich die Aktion viel schneller fort als normal. Wenn der Aktionstrom nur ein Nebenprodukt eines chemischen Prozesses wäre, so dürfte kein Unterschied in der Leitungsgeschwindigkeit auftreten, weil die Geschwindigkeit eines chemischen oder eines Diffusionsprozesses durch die Metallbrücke nicht beeinflusst wird. Durch die Metallbrücke wird lediglich der elektrische Transport erleichtert, denn die Brücke schliesst einen Teil des Nerven kurz, wodurch der Aktionsstrom diese Strecke überspringt. Daneben hat HODGKIN Versuche angestellt, bei denen er die Nervenfaser in Paraffinöl legte, sodass nur eine dünne Schicht von Gewebeflüssigkeit an der Oberfläche des Nerven übrigblieb. Unter diesen Umständen war die Geschwindigkeit des Aktionsstroms stark herabgesunken. Die Geschwindigkeit der Aktionswelle ist demnach völlig abhängig von dem ohmschen Widerstand an der Aussenseite des Nerven, also von der Geschwindigkeit mit welcher der elektrische Transport in der Längsrichtung der Nervenfaser stattfinden kann. Wir müssen demnach den Aktionsstrom als den eigentlichen Funktionsträger, als den wesentlichen Übertragungsprozess betrachten. Keine chemische Theorie der Reizübertragung ist imstande, die Tatsachen befriedigend zusammenzufassen; nur die elektrische Theorie der Reizübertragung ergibt ein geschlossenes Ganzes.

Im Vorstehenden sind nur einige grundlegende Prozesse der Nervenaktion gestreift worden, andere, wie z.B. die Refraktärzeit, die Prozesse bei der unterschwelligen Reizung usw, blieben unbeachtet. Es war nur die Absicht, durch eine bestimmte Anordnung von bekannten Tatsachen die Funktion des peripheren Nerven zu betrachten als das Resultat seiner charakteristischen Struktur, mit Hilfe derer das lebende Protoplasma imstande ist, aus dem Milieu aufgefangene Reize auf die reagierenden Organe zu übertragen.

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CONTRIBUTIONS TO THE COPEPOD FAUNA OF THE NETHERLANDS

BY

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I. HARPACTICOIDA COLLECTED ON OYSTERS IN THE EASTER SCHELDT

The present report is mainly based on material found on oysters of the Easter Scheldt. It has been collected by Dr P. Korringa, who kindly put his samples at my disposal. His collections were made in the period 12th–XII–1939 – 26th–X–1942 and contained 27 species, 17 of which are new to our fauna, viz:

Canuella furcigera G.O.Sars
Ectinosoma gothiceps Giesbr.
Ectinosoma melaniceps Boeck
Harpacticus obscurus Scott
Alteutha interrupta (Goodsir)
Parategastes sphaericus (Claus)
Dactylopusia latipes Boeck
Dactylopusia micronyx G.O.Sars
Parathalestris intermedia Gurney
Amphiascus debilis (Giesbr.)
Amphiascus similis (Claus)
Amphiascus tenellus G.O.Sars
Mesochra pygmaea (Claus)
Asellopsis intermedia Scott
Laophonte curticauda Boeck
Laophonte elongata Boeck
Metis ignea Philippi

In my descriptions I followed chiefly the well known excellent monographs of Sars (1911, 1921) and Gurney (1932); the figures are originals drawn from specimens occurring in the samples. The tables at the end show the numbers of specimens found in each of the quantitative samples of oysterpits near Yerseke.

Fam. LONGIPEDIIDAE

1. *Longipedia minor* Scott (figs. 1–5)

Female.–Margin of the segments with delicate spines and with some longer slender setae.1) Anal operculum with a strong spine in the middle and 6 spines at the side, diminishing in

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1) Giesbrecht (1881) mentions these setae, Sars probably has not seen them; in all my specimens they occur.

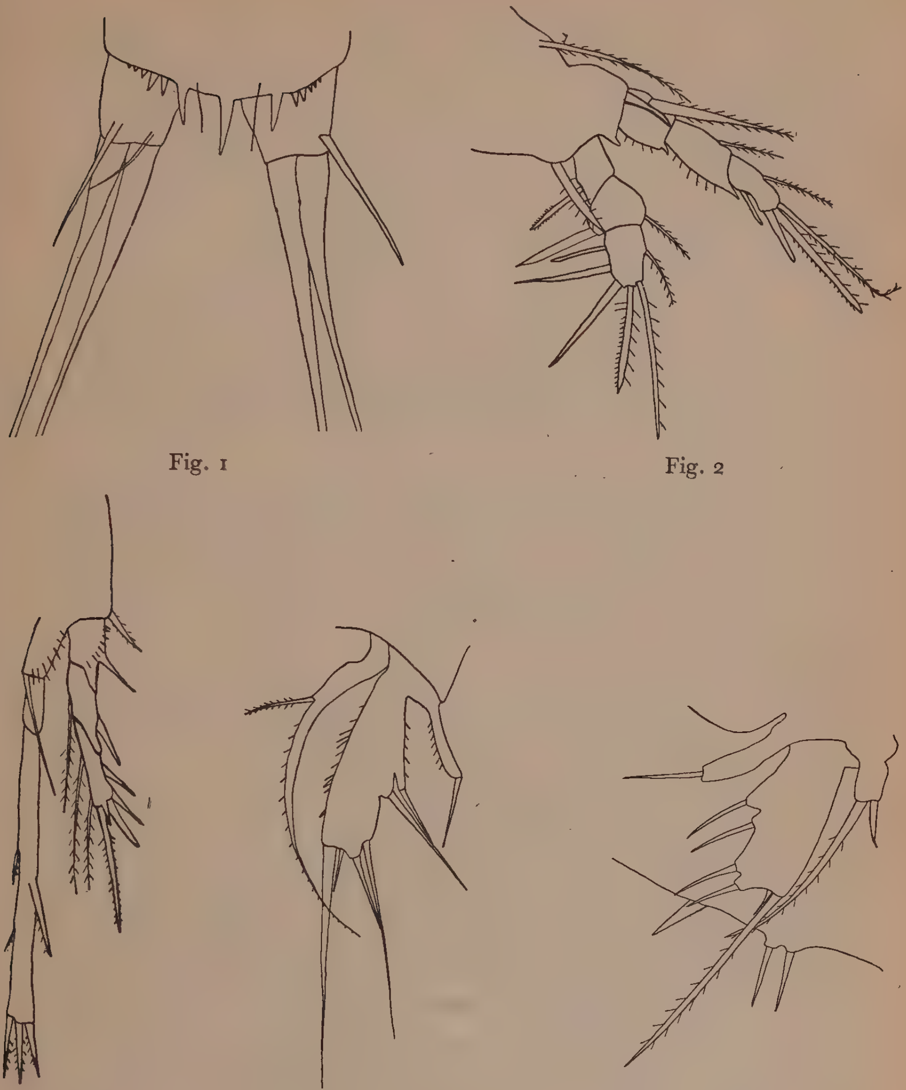


Fig. 1
Fig. 2
Fig. 3
Fig. 4
Fig. 5

Figs. 1–5. – *Longipedia minor* Scott

Female: Fig. 1 – Anal operculum and furca. × 290. (Yerseke Bank, 26–VI–1941).
Fig. 2 – P_1. × 290 (ibid.).
Fig. 3 – P_2. × 153 (ibid.).
Fig. 4 – P_5. × 290 (ibid.).
Male: Fig. 5 – P_5. × 270 (ibid.).

size (fig. 1). Rostrum short and broad, eye well developed. Antennulae rather robust, much curved of 5 imperfectly defined articulations with strong setae, some of which are plumose, others spiniform and strongly pectinate. Antennae: outer ramus as long as the inner and very flexible, of 6 segments. Natatory legs with both rami 3–articulate armed outside with strong spines, inside and at the tip with long partly spiniform setae. P_1 much smaller than the succeeding ones (fig. 2). P_2 with the inner ramus greatly elongated, the last joint almost 3 times as long as the first two joints combined, armed with 3 thick apical spines and 3 marginal ones, two at the innerside and one at the outerside, at about the middle of the joint (fig. 3). P_5 with distal joint rather elongate, ending with four spines, the two innermost shorter and two further spines near the middle of the inner edge (fig. 4).

Male.–Not differing much in external appearance from female. Apical setae not smooth as in female, but very conspicuously ciliated. P_5 with distal joint much shorter than in female ending with 4 spines, the innermost but one very short (fig. 5). Sixth segment with 3 spines, one lateral and two near the middle of the segment.

Length of female 0.81 mm, of male 0.73 mm.

Occurrence: Yerseke Bank, Easter Scheldt near Bergen op Zoom on oysterbeds and in pits; very abundant.

2. *Canuella furcigera* Sars (figs. 6–7)

Female.–Nearly cylindrical with thin and flexible integuments. Anal operculum simple, rounded. Caudal rami elongated, more than four times longer than broad, as long as two and a half abdominal segment, greatly divergent and with a wellmarked carina along the dorsal face. Rostrum well developed. Antennulae of 5 segments, resembling those of Longipedia. Antennae with the outer ramus fully as long as the inner, some of the setae very strong, almost spiniform. Outer ramus very strong, 7-articulate, inner ramus 2-articulate. Natatory legs with 3-articulate endo- and exopod, first pair shorter than the succeeding ones. P_5 very minute each forming a thin plate edged with 4 setae, the innermost but one the longest and distinctly plumous (fig. 6). Genital segment with 2 small juxtaposed lanceolate lappets below (fig. 7).

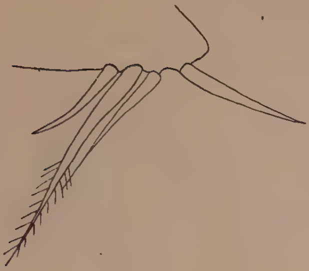


Fig. 6

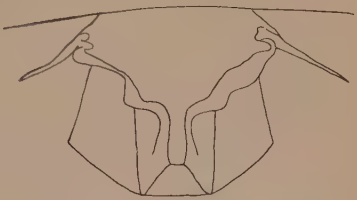


Fig. 7

Figs. 6–7. – *Canuella furcigera* Sars

Female: Fig. 6 – P_5. × 700 (Oysterpit near Yerseke, 6–XI–1941).
Fig. 7 – Genital area. × 190 (ibid.).

Length 1.05–1.24 mm.
Occurrence: Easter Scheldt near Yerseke, in oysterpits, from August till December.

Fam. ECTINOSOMIDAE

3. *Ectinosoma gothiceps* Giesbr. (figs. 8–9)

Female.–Body more or less slender, spoolform, with the anterior division scarcely broader than the posterior. Rostral plate of moderate size, not articulated to head, obtusely acuminate at the tip. Caudal rami very short, nearly as long as broad. Antennulae short with 6 joints. Antennae with 3 articulated outer rami. First pair of natatory legs scarcely smaller than the others, all the legs with 3 articulated exo -and endopod. P_5 (fig. 8) rather small with the marginal spines very long and considerably thickened at the base. Basal part with 2 setae, terminal joint threelobated, each lobe with a thick seta. One ovisac. Colour whitish gray (in preserved state).
Length 0.45 mm.

Male.–Not differing much in habitus from the female. Antennulae last joint but one swollen. P_5 (fig. 9) basal part ending with a long spine thickened at the base and a small one, terminal joint with four spines, the uttermost but one long and slender, the others more or less thickened at the base.
Length 0.40 mm.
Occurrence: Yerseke Bank near Yerseke.

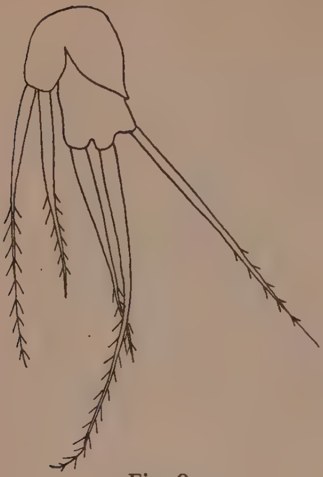


Fig. 8

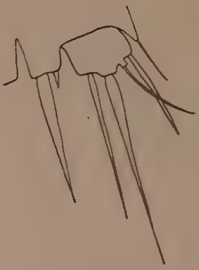


Fig. 9

Figs. 8–9. – *Ectinosoma gothiceps* Giesbr.
Female: Fig. 8 – P_5. × 370 (Yerseke Bank, 26–VI 1941).
Male: Fig. 9 – P_5. × 500 (Oysterpit near Yerseke, 5–X–1942).

4. *Ectinosoma melaniceps* Boeck (figs. 10–11)

Female.–Body resembling that of the above mentioned species. Its name is due to the dark shades occupying the cephalic segment.

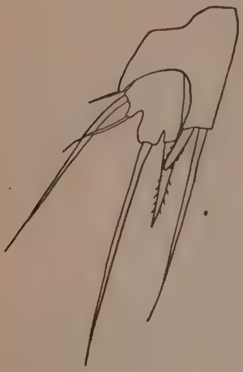


Fig. 10

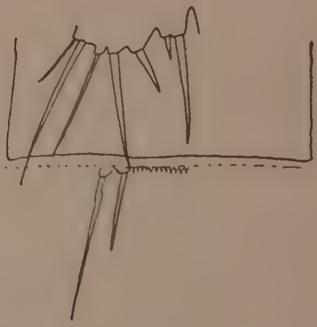


Fig. 11

Figs. 10–11. – *Ectinosoma melaniceps* Boeck
Female: Fig. 10 – P_5. × 290 (Oysterpit near Yerseke. 1–IX–1941).
Male: Fig. 11 – P_5. × 415 (Oysterpit near Yerseke, 29–IX–1942).

Rostral plate obtusely rounded at the top. Caudal rami about as long as they are broad, innermost apical seta very long. Antennulae 7-articulated. Legs 1–4 with 3-articulated exo- and endopod. P_5 (fig. 10) with basal part ending with a long slender spine and a short strongly denticulated spine, terminal joint with 2 unequal spines, at top a very slender hair and a long slender spine near the upper margin. Colour whitish with the above mentioned dark shade at the cephalic segment.

Male.–Not differing much in habitus from female. P_5 (fig. 11) basal part with a short and a long spine, terminal joint with four setae, the innermost rather short. P_6 a short plate with two unequal spines.

Occurrence: Easter Scheldt near Yerseke and Bergen op Zoom, on oysterbeds.

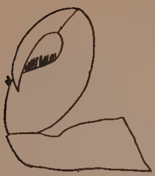
Fam. HARPACTICIDAE

5. *Harpacticus obscurus* T. Scott (figs. 12–18)

Female.–Body slender, the anterior part broader than the posterior. Furca short, broader than long. Rostrum mobile marked of from the head, broad, the end with on each side a short hair. Antennulae of 9 segments, the terminal part consists of 5 small articulations, which together are longer than joint 3. Antennae robust, 2-articulated, with 2-jointed exopod ending with one short and two longer setae, the inner ramus with 3 strong claw-like spines and 4 geniculated setae. Maxilliped (fig. 12) subcheliform, the edge of distal joint with spines. First pair of legs (fig. 13) with both rami prehensile and very unequal, the exopod much the longer, 3-articulated and armed at the tip with 3 curved claws, the endopod 2-articulated, with two claws at tip. P_{2-4} both rami with 3 joints, the exopod the longer. Last pair of legs (fig. 14) lamellar, basal part ending with 4 setae, terminal joint somewhat longer than the basal part, ending with 2 long setae and 3 spines. Genital area (fig. 15).

Length: 0.66 mm.

Male.–Somewhat larger than female. Antennulae very strong. Endopod of 2nd pair of legs (fig. 16) with the middle joint produced to a long projection reaching far behind the end of the third joint. P_3 (fig. 17) with very strong exopod, each joint denticulated along its margin, the last segment ending with 3 robust spines, a strong seta and 4 slender setae on the inner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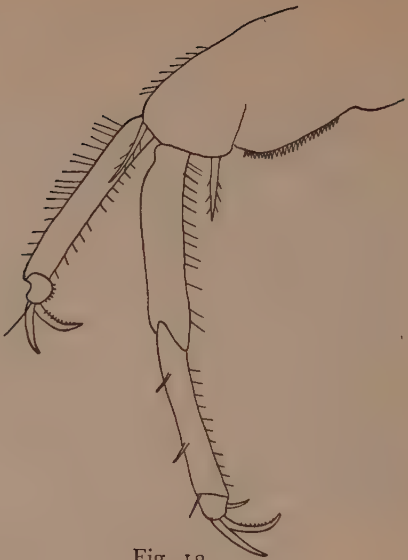
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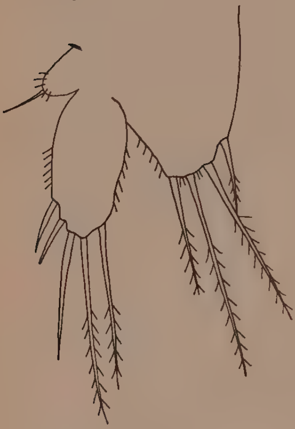
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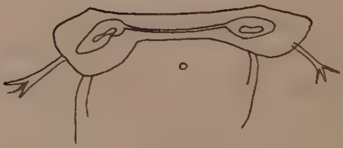
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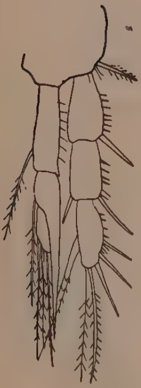
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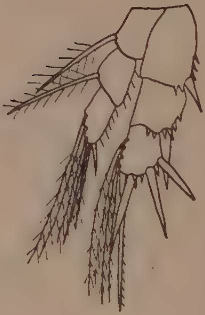
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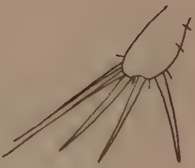


Fig. 18

Figs. 12–18. – *Harpacticus obscures* Scott

Female: Fig. 12 – Maxilliped. × 290 (Oysterpit near Yerseke, 4–XII–1941).
Fig. 13 – P_1. × 290 (ibid.).
Fig. 14 – P_5. × 375 (ibid.).
Fig. 15 – Genital area. × 375 (ibid.).
Male: Fig. 16 – P_2. × 180 (Oysterpit near Yerseke, 10–VI–1942).
Fig. 17 – P_3. × 180 (ibid.).
Fig. 18 – P_5. × 320 (ibid.).

margin. P_5 (fig. 18) with a long club-like terminal part ending with 3 strong setae and two slender ones.

Occurrence: On oysterbeds in the Easter Scheldt near Yerseke.

Fam. PELTIDIIDAE

6. *Alteutha interrupta* (Goodsir) (figs. 19–22)

Female.–Body (fig. 19) oval in outline, somewhat vaulted above and capable of rolling itself into a ball, with the lateral parts of the cephalic segments inflexed ventrally, rostrum immobile, not marked of from the head. Urosome short and broad, generally bent downwards. Caudal rami short and broad. Antennulae 8-articulate. Maxilliped (fig. 20) with narrow hand oblong in form tipped with a claw not reaching the beginning of the hand. P_1 (fig. 21) rather slender, both rami

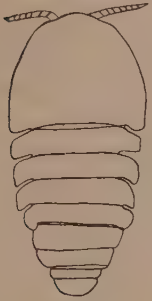


Fig. 19

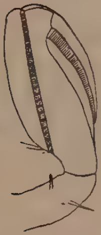


Fig. 20

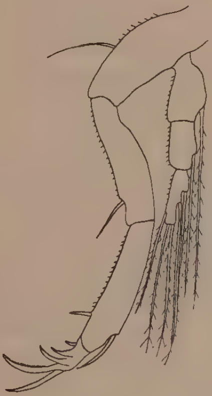


Fig. 21

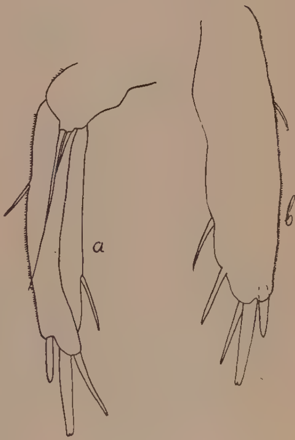


Fig. 22

Figs. 19–22. – *Alteutha interrupta* (Goodsir)

Female: Fig. 19 – Dorsal view. × 38 (Oysterpit near Yerseke, 31–VII–1941).
Fig. 20 – Maxilliped. × 190 (ibid.).
Fig. 21 – P_1. × 190 (ibid.).
Fig. 22 – P_5. × 190, a, side view; b, dorsal view (ibid.).

with 3 joints, exopod with joint 1 and 2 equal in length, last joint very short and provided with 5 claws gradually increasing in length inwards, endopod much shorter than exopod, all the joints with long setae. P_{2-4} both rami tri-articulate with long setae. P_5 (fig. 22) basal part very short, terminal joint oblong, flattened with 3 strong spines at the tip and 2 smaller ones on the outer edge. One ovisac.

Length of adult female 1.2 mm.

Male.–Differing but little from female in external appearance, easily recognizable by the more strongly built and prehensile anterior antennulae.

Occurence: In the Easter Scheldt near Yerseke, on oysterbeds, very abundant.

Fam. TEGASTIDAE

7. *Parategastes sphaericus* (Claus) (fig. 23)

Female.–Body, seen lateraly, almost circular in outline, the back much curved and the genital segment greatly produced below. Outer segments of urosome very short and retractile. Cephalic segment with a well-marked chitinous stripe across the back, postero-lateral corners moderately produced, rostrum slightly prominent at the tip. Genital segment produced below to a rather massive nearly quadrangular prominence: the anterior corner tongue-shaped, the posterior unguiform and recurved, and exhibiting in the middle, between the two, a smaller recurved dentiform projection on each side. Antennulae slender with 7 joints. Antennae with 3-articulate inner ramus and small exopod, at tip with two setae. First pair of legs with both rami short, uniarticulate. Natatory legs with slender rami, the endopod the longer and 3-articulate, the exopod with two joints. P_5 of female very large, with basal joint broad and vaulted, the terminal part small, with a short spine at the tip, the outer margin with 4 setae (fig. 23).

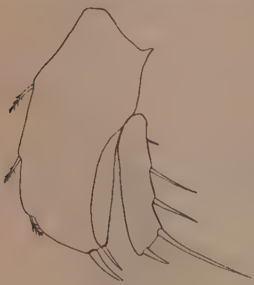


Fig. 23. – *Parategastes sphaericus* (Claus)

Female: Fig. 23 – P_5. × 250 (Oysterpit near Yerseke, 31–VII–1941).

Male.–Resembling the female, antennulae prehensile with the 4th joint large, the last claw-shaped. Last pair of legs very narrow, the proximal joint not expanded, distal joint linear, with 2 slender setae at the end.

Length 0.41 mm.

Occurrence: Easter Scheldt on oysterbeds near Yerseke.

Fam. IDYIDAE

8. *Tisbe* (*Idya*) *furcata* (Baird) (figs. 24–28)

Female.–Body moderately slender, distinctly depressed with the anterior and posterior divisions sharply defined. Rostral projection short and obtuse, not marked of from head. Caudal rami short. Antennulae 8–articulate, sensory filament of 4th joint very fully developed (fig. 24). Antennae inner ramus with 3 joints, the exopod 4-segmented. First pair of legs (fig. 25) robust, both rami 3-articulate, unequal in size and structure, the endopod the longer, the second segment more or less prolonged, the distal very small ending in 2 small claws; the exopod with the distal joint provided at the inner corner with 2 slender ciliated setae, and along the truncated end with 4 outward curving spines gradually increasing in length, clothed on one edge with a limited number of long cilia. Legs 2–4 both rami 3-segmented provided with strong broad spines and long ciliated setae, these are bi-articulate (fig. 26), they have a stiff quill on both sides with short stiff hairs and a long thin end with thin hairs on both sides. Only GIESBRECHT (1881) gives a drawing of those setae, SARS nor other investigators mention those bi-articulated setae. Last pair of legs with very long terminal joint, with 4 setae at tip, one at a quarter of the distance from the tip, basal part short and broadly rounded ending with a long spine and at each side of this a short spine. (fig. 27).

Male.–Much smaller than female, antennulae strongly built, distinctly geniculate. In the 2nd pair of legs, the seta of the first joint of the inner ramus is modified into a very strong, ciliated spine (fig. 28). Last pair of legs of smaller size than the female, has one of the apical setae of the distal joint transformed in a long ciliated spine.

Length ♂ and ♀ 0.81–0.91 mm.

Occurrence: On oysterbeds near Yerseke and Bergen op Zoom.

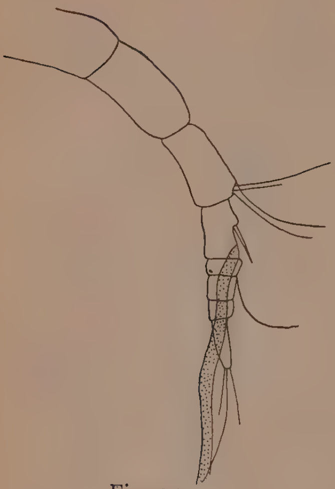


Fig. 24

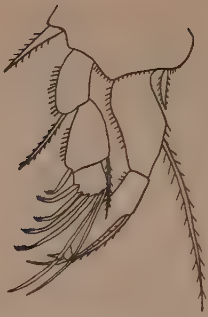


Fig. 25

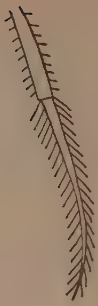


Fig. 26

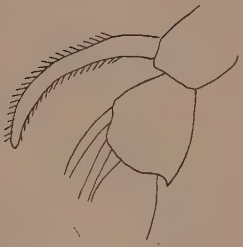


Fig. 28

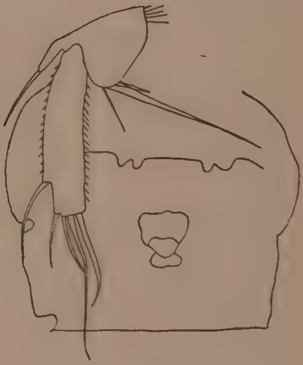


Fig. 27

Figs. 24–28. – *Tisbe (Idya) furcate* (Baird)

Female: Fig. 24 – Antennula. × 230 (Yerseke Bank, 26–VI–1941).
Fig. 25 – P_1. × 230 (ibid.).
Fig. 26 – Seta of leg 2. × 440 (ibid.).
Fig. 27 – P_5. and genital area. × 230 (ibid.).
Male: Fig. 28 – P_2. Spine on endopod-joint 1. × 320 (ibid.).

Fam. THALESTRIDAE

9. *Dactylopusia latipes* Boeck (figs. 29–33)

Female.–Body very robust, with the anterior part considerably dilated and of rounded oval form. Rostrum marked of from body. Urosome much narrower. Caudal rami very short, nearly twice as broad as they are long; they are provided with two long setae the innermost at the base with a very conspicuous dilatation. (fig. 29). Antennulae short and thick. Antennae with 2-segmented inner ramus and 3-articulate exopod. First pair of legs (fig. 30) very robust, both rami 3-articulate the exopod extending scarcely to the end of the first joint of the endopod; exopod ending with 5 claws diminishing in length from inner to outer edge, the two last segments of endopod nearly equal in length and the distal one ending with 2 strong claws. Legs 2–4, both rami 3-articulate, strongly built, provided with long ciliated setae and strong spines. P_5 (fig. 31) basal part broad

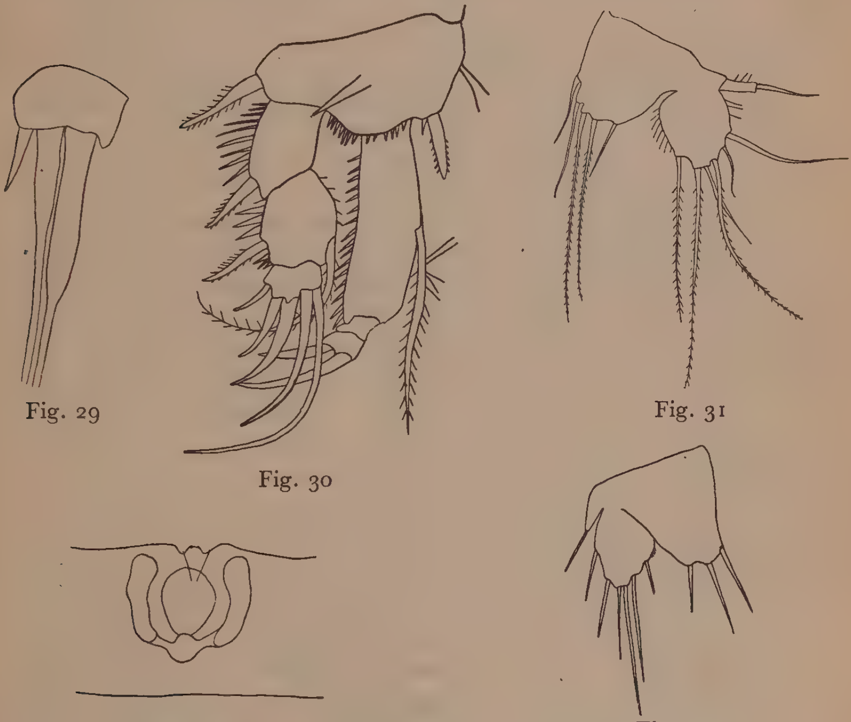


Fig. 29
Fig. 30
Fig. 31
Fig. 32
Fig. 33

Figs. 29–33. – *Dactylopusia latipes* Boeck

Female: Fig. 29 – Part of furca with end setae. × 370 (Yerseke Bank, 26–VI–1941).
Fig. 30 – P_1. × 370 (ibid.).
Fig. 31 – P_5. × 250 (ibid.).
Fig. 32 – Genital area. × 370 (ibid.).
Male: Fig. 33 – P_5. × 320 (Oysterpit near Yerseke, 20–VII–1942).

nearly as long as terminal part ending with 5 setae, terminal joint with 6 setae. Genital area (fig. 32).

Length 0.75 mm.

Male.-General form much less dilated than in female. Furcal rami short and broad, ending with two long setae and a shorter one, at the outer edge a short spine. The innermost but one of the apical setae not dilated at the base as is the case in the female. Margin of the caudal rami denticulated, anal opercle ending with a short spine. P$_2$ inner ramus with a strong spine. P$_5$ (fig. 33) basal part with 3 spines, terminal joint with six setae. P$_6$ a short plate with 3 setae, the innermost the longer and diminishing in size to the side-border of the segment.

Length 0.62 mm.

Occurrence: Oysterbeds near Yerseke in the Easter Scheldt.

10. *Dactylopusia micronyx* Sars (figs. 34–36)

Female.–Body rather slender, somewhat tapering behind. Caudal rami much shorter than broad. Antennulae 8–9 articulate, penultimate and antipenultimate joints not always distinctly defined. First pair of legs (fig. 34) with the exopod short and stout, the terminal joint short and provided with 5 claws,

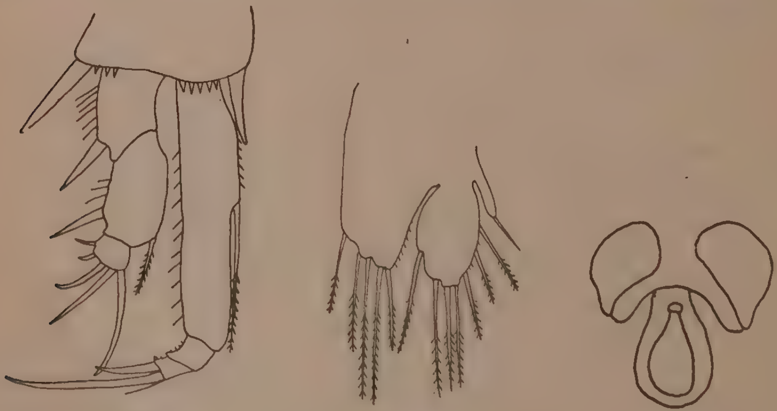


Fig. 34 Fig. 35 Fig. 36

Figs. 34–36. – *Dactylopusia micronyx* Sars

Female: Fig. 34 – P$_1$. × 430 (Oysterpit near Yerseke, 8–VII–1942).
Fig. 35 – P$_5$. × 320 (ibid.).
Fig. 36 – Genital area. × 640 (ibid.).

the two outer ones very short. Endopod with a long proximal part, longer than the entire exopod; the last two joints short, equal in length, the terminal part ending with 2 claws and a small seta. P_5 (fig. 35) basal part ending with 5 plumose setae, the distal part with seven. Genital area (fig. 36). Colour in preserved specimens blue.

Length 0.65 mm.

Occurrence: Oysterbeds near Yerseke in the Easter Scheldt.

11. *Parathalestris intermedia* Gurney (figs. 37–45)

Female.–Body rather slender, cephalothorax much longer than the following 4 segments together. Rostrum large, distinctly marked off from head. The somites 1–4 of abdomen with a short oblique lateral row of spines. Furcal rami little more broad than long with an oblique row of spines on inner side dorsaly. At outer angle a spine, dilated at base and tapering to a hair (fig. 37). Inner and outer terminal setae rather short and slender. Anal operculum smooth. Antennulae of 9 segments. Antennae (fig. 38) indistinctly 3–segmented with 3 finely pectinated setae and four broken spines. Exopod 2–articulate, at tip with 2 nearly equally long setae. Maxilliped (fig. 39) with narrow palm, anterior surface with several rows of stiff hairs, a long seta somewhat in the middle of the inner edge; claw as long as palm. Leg 1 (fig. 40) endo- and exopod prehensile, exopod only slightly shorter than endopod. Terminal claws stout. Legs 2–4 both rami 3–segmented, the outer one the longer. P_5 (fig. 41) basal part produced to end of terminal segment, broad and bearing at the tip five ciliated setae, the third (from outside) the longer, the proximal part with a long seta and a row of strong spines (fig. 42). Terminal joint oval with six setae, 2 and 3 (from inside) are bare, the others ciliated.

Length 1.2 mm.

Male.–Outer appearrance resembling the female. Leg_1 (fig. 43) inner spine of basipod modified, curved inwards. Leg_2 with endopod normally 2–segmented, last segment (fig. 44) with two smooth, broad setae on outer margin and a short curved feathered seta near apex. Apex pointed. I have also found males with 3-segmented endopod as Gurney mentions in his publication. (Gurney, 1930). P_5 (fig. 45) with basal segment scarcely produced, with 3 setae and terminal part with 5 pectinate setae and one hair. P_6 three short spines on each side of segment 6. The furca of the male is not provided with a dilated spine as in the female, but only with a strong spine.

Length 1 mm.

Occurrence: Rather abundant on oysterbeds near Yerseke.

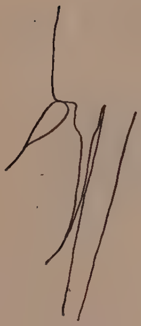


Fig. 37

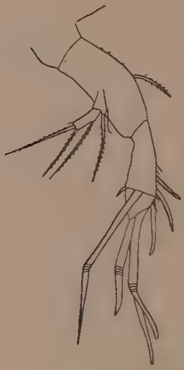


Fig. 38

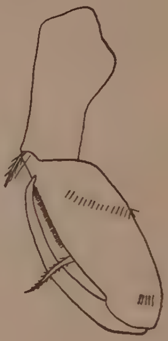


Fig. 39

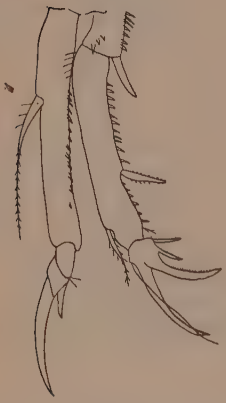


Fig. 40

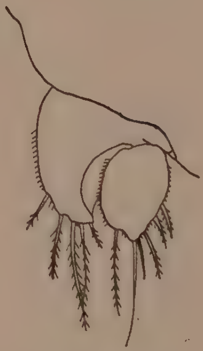


Fig. 41

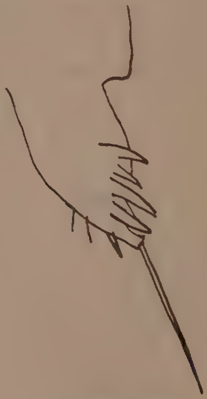


Fig. 42

Figs. 37–45. – *Parathalestris intermedia* Gurney

Female: Fig. 37 – Furcal setae. × 370 (Oysterbed 417, 8–V–1941).
Fig. 38 – Antenna. × 190 (ibid.).
Fig. 39 – Maxilliped. × 290 (ibid.).
Fig. 40 – P_1. × 190 (ibid.).
Fig. 41 – P_5. × 110 (ibid.).
Fig. 42 – P_5. proximal part of basale. × 580 (ibid.).

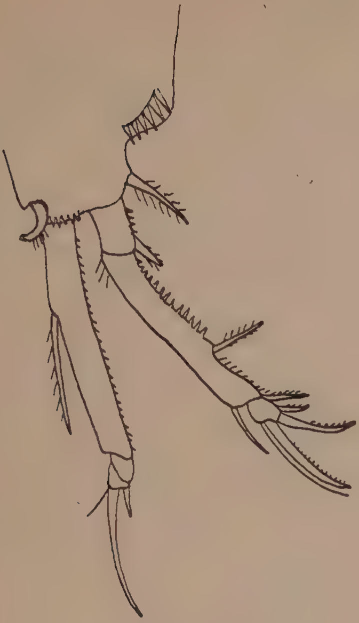


Fig. 43

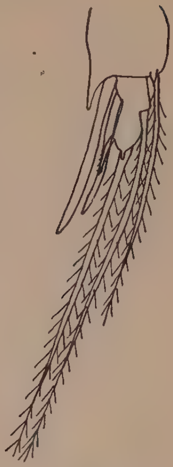


Fig. 44

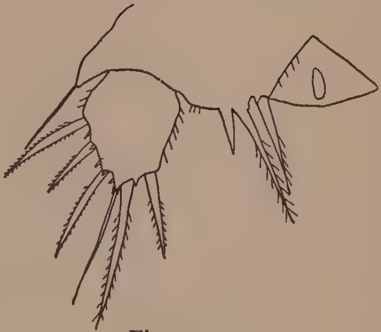


Fig. 45

Parathalestris intermedia (continued)

Male: Fig. 43 – P_1. × 220 (ibid.).
Fig. 44 – P_2. last segment of endopod. × 290 (ibid.).
Fig. 45 – P_5. × 290 (ibid.).

12. *Thalestris longimana* Claus (figs. 46–52)

Female.–Body very robust with the back more or less curved (fig. 46). Cephalic segment very large, rostrum short and blunt at the tip, not marked of from the head. Urosome scarcely exceeding half the length of the anterior division and with very sharply defined segments. Genital segment (fig. 50) large and broad, quadrangular in form, with the lateral parts lamellarly expanded. Caudal rami rather short, not much longer then they are broad, truncated at tip. Eye large and of very conspicuous

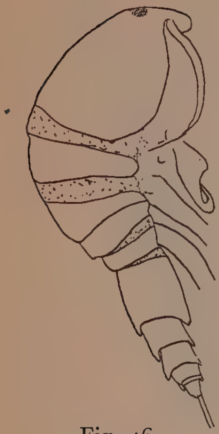


Fig. 46

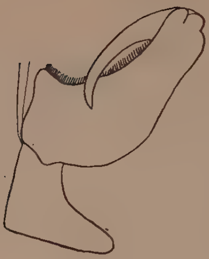


Fig. 47

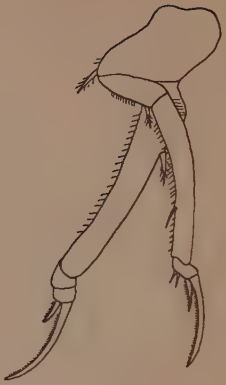


Fig. 48

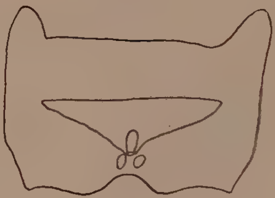


Fig. 50

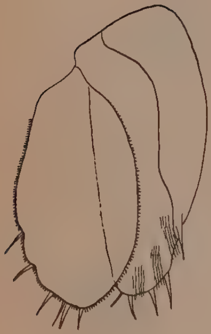


Fig. 49

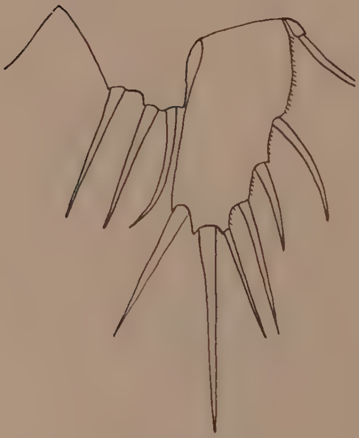


Fig. 52

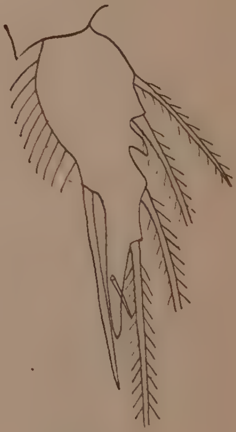


Fig. 51

Figs. 46–52. – *Thalestris longimana* Claus

Female: Fig. 46 – Side view. × 44 (Oysterpit near Yerseke, 4–XII–1941).
Fig. 47 – Maxilliped. × 110 (ibid.).
Fig. 48 – P_1. × 110 (ibid.).
Fig. 49 – P_5. × 110 (ibid.).
Fig. 50 – Genital area. × 110 (ibid.).
Male: Fig. 51 – P_2. last segment of endopod. × 290 (ibid.).
Fig. 52 – P_5. × 290 (ibid.).

blue colour. Antennulae 9-articulate. Antennae three-articulate, exopod with 2 segments. Maxilliped (fig. 47) powerfull, with broad palm at the edge with short stiff hair, claw very strong not reaching the end of the palm. P_1 with both rami of equal length, the exopod somewhat narrower than the endopod, each ramus armed with 2 unequal claws finely denticulate along the concave edge (fig. 48). P_{2-4} with both rami 3-articulate. P_5 (fig. 49) exceedingly large, extending beyond the limits of the genital segment, terminal part oblong oval, basal part with 3 rows of spines near the base; marginal setae of both joints short and simple. Genital area (fig. 50).

Length 1.4 mm.

Male.–Somewhat smaller than female. Last segment of endopod of P_2 (fig. 51) with a broad seta and a strong spinelike processus at the tip. P_5 (fig. 52) terminal part much longer than basal joint, broadly linear at outer margin and at the tip with strong spines, basal part with 3 long spines.

Length 1.2 mm.

Occurrence: In Easter Scheldt, on oysterbeds.

Fam. DIOSACCIDAE

13. *Diosaccus tenuicornis* (Claus) (figs. 53–59)

Female.–Body moderately robust, with the anterior division considerably broader than the posterior. Rostrum very prominent, marked off from head in lateral view with a little hook at the tip (fig. 53). Caudal rami short, slightly longer than they are broad. Antennulae 8 segmented, the four last joints a little longer than the fourth joint, the latter with a broad sensorial seta (fig. 54). Antennae rather slender, 2-segmented with the terminal joint long and narrow, exopod with 1 segment which has 4 setae, 2 apical and 2 lateral. Maxilliped (fig. 55) with large palm, deeply concave inside, claw strong and curved. P_1 (fig. 56) exopod half of the length of the endopod. Proximal part of endopod very long, the outer 2 joints short, apical claws slender and very unequal. Distal part of exopod with 3 spines successively increasing in length and a long seta at the inner corner. P_{2-4} both rami 3-articulate. Last pair of legs (fig. 57) basal and terminal part nearly equal in length, basal joint narrow linguiform in shape with 5 marginal setae, the middle one very thin, the others thick, spiniform and coarsely dentic-

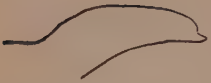


Fig. 53

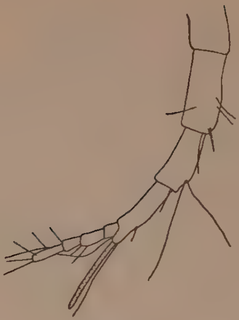


Fig. 54

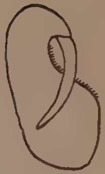


Fig. 55

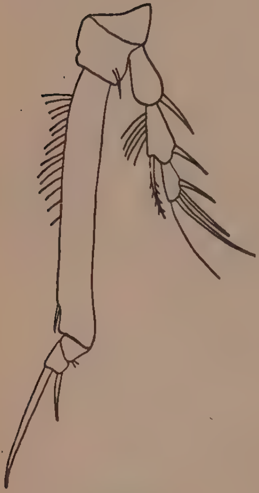


Fig. 56

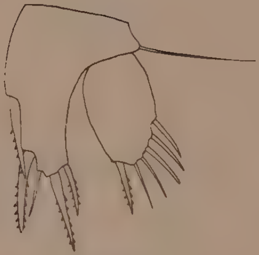


Fig. 57

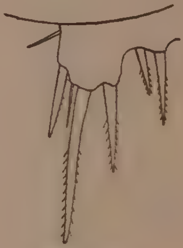


Fig. 58

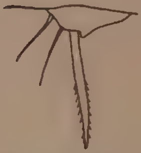


Fig. 59

Figs. 53–59. – *Diosaccus tenuicornis* (Claus)

Female: Fig. 53 – Rostrum. × 290 (Oysterpit near Yerseke, 4–XII–1941).
Fig. 54 – Antennula. × 190 (ibid.).
Fig. 55 – Maxilliped. × 290 (ibid.).
Fig. 56 – P_1. × 290 (ibid.).
Fig. 57 – P_5. × 250 (ibid.).
Male: Fig. 58 – P_5. × 320 (Oysterpit near Yerseke, 10–VIII–1942).
Fig. 59 – P_6. × 320 (ibid.).

ulated. The terminal part oblong, provided with 6 spines, the innermost thick and with coarse denticules.

Length 0.80 mm.

Male.–Much smaller than female, exhibiting the usual sexual differences. First pair of legs with a small linguiform lappet inside the second basal joint. P_2 with the inner ramus very short, scarcely as long as the first joint of the exopod, distal part rounded and ending with a curved finger-like projection and a plumose seta. Last pair of legs (fig. 58) with the basal part very flat ending with two plumose spines, the terminal part with 3 strong plumose spines and a short slender seta. P_6 (fig. 59) with a strong spine and two slender setae.

Length 0.58 mm.

Occurrence: Easter Scheldt near Yerseke and Bergen op Zoom, on oysterbeds.

14. *Amphiascus debilis* (Giesbr.) (fig. 60)

Female.–Body slender, rostrum well developed, caudal rami very short, being about twice as broad as they are long, middle apical setae slightly thickened at the base. Antennulae with 8 joints. First pair of thoracic feet with the outer ramus extending somewhat beyond the middle of the first joint of the inner branch, last joint of the exopod twice as long as the second, and ending with two claws and a short seta. Legs 2–4 the median part of the endopod in each provided with one seta. Last pair of legs (fig. 60) with the terminal part oval in form, provided with 5 setae, that one issuing from the top very slender and quite smooth; basal part large with a distinct hole in the inner margin, extending about as far as the terminal joint, with 2 setae at the top and 3 marginal ones.

Length 0.50 mm.

Occurrence: Oysterbeds near Yerseke.

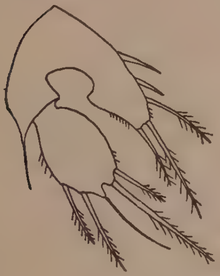


Fig. 60. – *Amphiascus debilis* (Giesbr.)

Female: Fig. 60 – P_5. × 320 (Oysterpit near Yerseke, 16–VI–1942).

15. *Amphiascus similis* (Claus) (figs. 61–68)

Female.–Body very slender, only slightly tapering behind. Cephalic segment scarcely longer than the 3 succeeding segments combined; rostrum very long, marked of from the head. Anal operculum finely spinulose. Segments on the lateral side with rather strong spines. Caudal rami nearly quadrate in form, only slightly longer than broad. Antennulae 8-articulate. Antennae 2-segmented with 3-segmented exopod (fig. 61), the middle joint very small and without any seta. First pair of legs rather slender, endopod with long proximal joint, the 2 last segments equal in length and provided with 2 unequal claws; exopod not reaching the end of proximal joint of endopod, middle joint the longest, terminal joint small with 3 claw-like spines and a seta at the inner corner (fig. 62).

Legformule of P_{2-4}

	Exopod			Endopod		
Joint	1	2	3	1	2	3
P_2	1	1	2.2.3	1	2	1.2.1
P_3	1	1	3.2.3	1	2	3.2.1
P_4	1	1	2.2.3	1	1	2.2.1

Last pair of legs (fig. 63) with terminal part large oval of form, carrying 6 rather unequal setae; basal joint comparatively short, triangular, not nearly extending to the middle of the terminal part, marginal setae 5, the outermost one very small, the two following plumose. Genital area (fig. 64).

Length 1.48 mm.

Male.–Body more slender than in female. Antennulae transformed in the usual manner. First pair of thoracic feet with the inner corner of the second basal joint provided with a strong, at the top slightly bifurcated spine (fig. 65). The last joint of the inner ramus of the 2nd pair of legs ending with two strong transformed spines and two long plumose setae (fig. 66). Fifth pair (fig. 67), the basal part is provided with one very short and one longer spine, the terminal joint is nearly as long as broad and ends with 4 spines, two of them are rather short. Sixth pair with 3 spines, the innermost very short (fig. 68).

Length 0.85 mm.

Occurrence: On oysterbeds in the Easter Scheldt, near Yerseke en Bergen op Zoom.

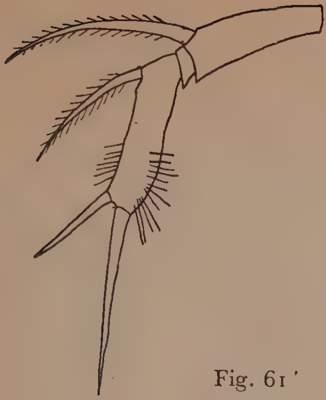


Fig. 61

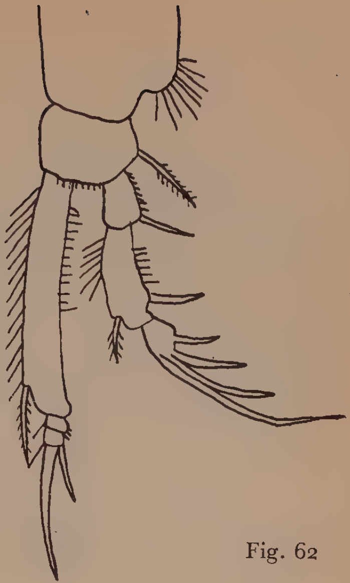


Fig. 62

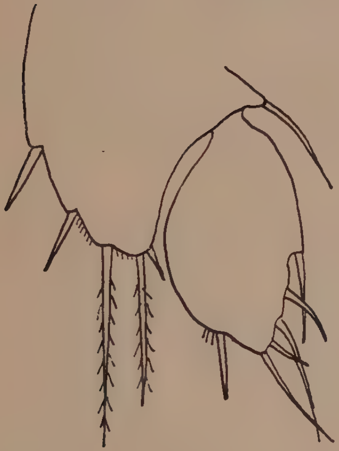


Fig. 63

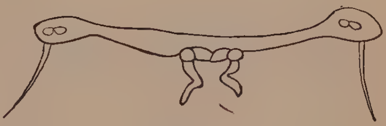


Fig. 64

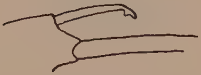


Fig. 65

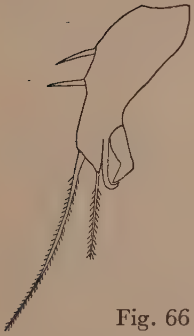


Fig. 66

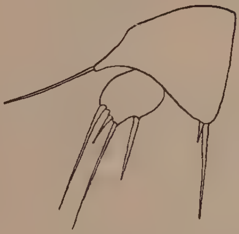


Fig. 67

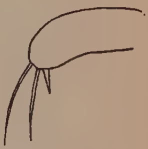


Fig. 68

Figs. 61–68. – *Amphiascus similis* (Claus)

Female: Fig. 61 – Antenna, exopod. × 550 (Oysterpit near Yerseke, 5–XII–1941).

Fig. 62 – P_1. × 220 (ibid.).

Fig. 63 – P_5. × 220 (ibid.).

Fig. 64. – Genital area. × 290 (ibid.).

Male: Fig. 65 – P_1., inner corner of 2nd basal joint. × 240 (Oysterpit near Bergen op Zoom, 6–VIII–1942).

Fig. 66 – P_2., last part of endopod. × 280 (ibid.).

Fig. 67 – P_5. × 240 (ibid.).

Fig. 68 – P_6. × 240 (ibid.).

16. *Amphiascus tenellus* Sars (figs. 69–76)

Female.–Body slender. Rostrum narrow, lanceolate. Caudal rami short. Antennulae (fig. 69) slender, 8-articulate, 2nd joint much the largest, 4th joint narrow, twice as long as third. First pair of legs (fig. 70) with the outer ramus much shorter than first joint of the inner branch, middle joint with a well developed seta inside, last joint nearly as long as second, armed with 3 spines and 2 geniculated setae; inner branch with the first joint very narrow, last joint more than twice as long as the second.

Legformule of P_{2-4}.

	Exopod			Endopod		
Joint	1	2	3	1	2	3
P_2	1	1	2.2.3	1	2	1.2.1
P_3	1	1	2.2.3	1	1	3.2.1
P_4	1	1	2.2.3	1	1	3.2.1

Last pair of legs (fig. 71) with terminal part oval in form, marginal setae 6, rather small; basal part triangular, extending beyond the middle of the terminal part, provided with a row of 5 setae. Genital area see fig. 72.

Length 0.66 mm.

Male.–Somewhat smaller than female. The second basal part of first pair of legs (fig. 73) armed inside with 2 closely-set spines in front of which a knob-like prominence. Inner ramus of second pair of legs transformed (fig. 74). P_5 (fig. 75) very small, basal part with 2 setae and a short tooth-like projection. Basal part short and broad ending with 5 setae. P_6 a plate provided with 3 spinules (fig. 76).

Length 0.58 mm.

Occurrence: In oysterpits near Bergen op Zoom and Yerseke.

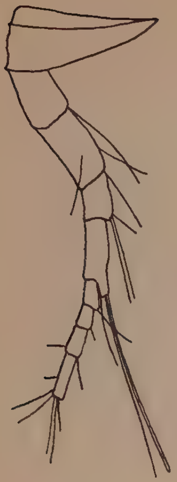


Fig. 69

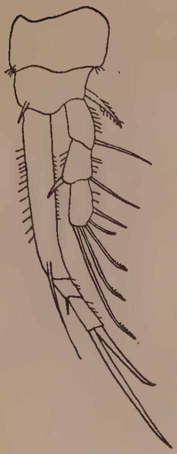


Fig. 70

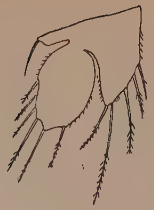


Fig. 71

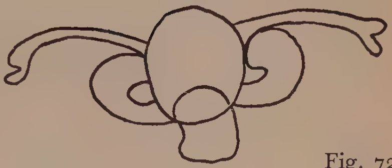


Fig. 72

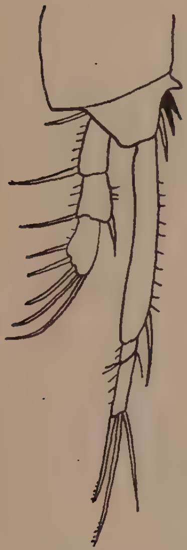
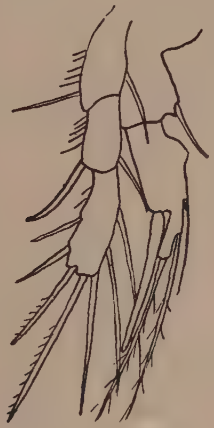


Fig. 73



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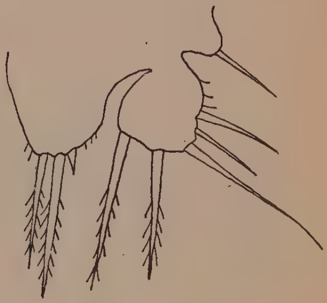

Fig. 75

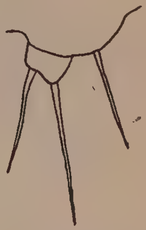

Fig. 76

Figs. 69–76. – *Amphiascus tenellus* Sars

Female: Fig. 69 – Antennula. × 240 (Oysterpit near Bergen op Zoom, 6–VIII–1942).
Fig. 70 – P_1. × 240 (ibid.).
Fig. 71 – P_5. × 180 (ibid.).
Fig. 72 – Genital area. × 1500 (ibid.).
Male: Fig. 73 – P_1. × 640 (ibid.).
Fig. 74 – P_2. × 1500 (ibid.).
Fig. 75 – P_5. × 1000 (ibid.).
Fig. 76 – P_6. × 360 (ibid.).

Fam. CANTHOCAMPTIDAE

17. *Mesochra lilljeborgi* Boeck

Female.–Body slender, rostrum long, triangular, marked off from head. Operculum smooth. Furcal rami 1½ times as long as broad. Antennulae 7-articulate. Antenna of 3-segments, exopod only one segment with 3 setae. Leg 1 with 2 segmented endopod, first joint longer than entire 3-segmented exopod. Legs 2–4 endopod 2–, exopod 3–segmented, exopod much the longer. Last pair of legs: basal part produced beyond terminal part, narrowed distally with 6 setae, the third (from inward) the longer. Terminal part a little longer than it is wide with 5 setae, the innermost but one the longer.

Length 0.73 mm.

Occurrence: On oysterbeds near Yerseke.

18. *Mesochra pygmaea* (Claus) (figs. 77–78)

Female.–Body moderately short and stout. Rostrum not prominent, not articulated to the head. Caudal rami very short, nearly as long as they are broad. Anal opercle with minute spines. Lateral side of the abdominal segments also with spines. Antennulae

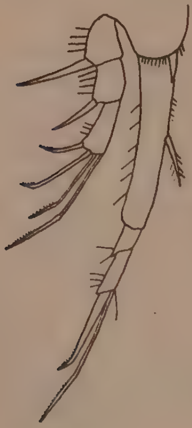

Fig. 77

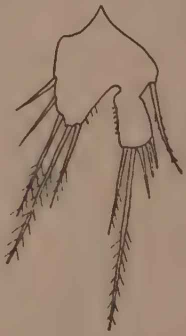

Fig. 78

Figs. 77–78. – *Mesochra pygmaea* (Claus)

Female: Fig. 77 – P_1. × 430 (Oysterpit near Yerseke, 10–VI–1942).
Fig. 78 – P_5. × 430 (ibid.).

composed of 6 segments. Antennae with outer ramus small, uni-articulate. In the first pair of thoracic feet (fig. 77) the outer branches scarcely more than half as long as the 3-articulated inner, this branch with the first joint very long, somewhat dilated at the base, seta of the inner edge attached above the middle. Last of the joints twice as long as the middle one, and ending with a short hair and two claws, the inner one shorter than the outer. Leg 2–4 with biarticulate endopod. In the fifth pair (fig. 78) the basal part provided with 5 setae, the distal part with 2 plumose setae and three rather short spines. Colour blue, in preserved condition.

Length 0.40 mm.

Occurrence: On oysterbeds near Yerseke.

19. *Nitocra typica* Boeck

Female.–Body very slender, with the anterior part scarcely broader than the posterior. Rostrum narrow, pointed in dorsal view, jointed to head. Segments of abdomen on dorsal side with row of spines, lateral spines very long. Operculum with about 9 long sharp spines. Furcal rami broader than long. Antennulae 8 segmented, antennae of 4 segments, the outer ramus one segment ending with 3 setae. Legs 1–4 with both rami 3 segmented. First pair of legs with segment 1 of endopod as long as whole exopod. P_5 terminal part longer than wide, rather parallelsided with 6 setae, the basal part reaches only till the half of terminal segment, is provided with 5 setae, the innermost but one the longer.

Length 0.70 mm.

Occurrence: On oysterbeds near Yerseke.

20. *Ameira parvula* Claus (figs. 79–80)

Female.–Body slender, sublinear in form, rostral projection very small. Caudal rami about as long as they are broad. Antennulae 8-segmented. Antennae of 3 joints, outer ramus small, uniarticulate. First pair of legs with the outer ramus about half the length of the inner, terminal joint of endopod very slender, linear in form, about 3 times as long as the second, both together nearly as long as the proximal segment (fig. 79). P_{2-4} with both rami 3-segmented. Last pair of legs (fig. 80) with terminal part

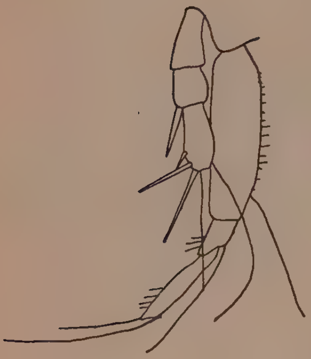

Fig. 79

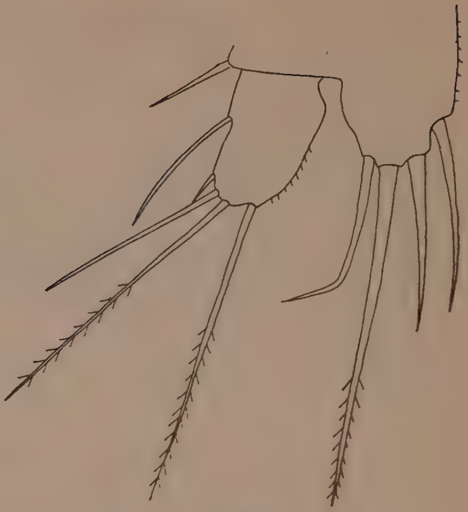

Fig. 80

Figs. 79–80. – *Ameira parvula* Claus

Female: Fig. 79 – P_1. × 380 (Yerseke Bank, 26–VI–1941).
Fig. 80 – P_5 × 560 (ibid.).

nearly twice as long as basal part, the last ending with 4 setae, the innermost but one the longer; terminal joint with 5 setae.

Male.–Basal part of leg 5 not much pronounced, ending with two short setae, terminal part small with 3 spines.

Length 0.50 mm.

Occurrence: On oysterbeds near Yerseke.

Fam. LAOPHONTIDAE

21. *Laophonte curticauda* Boeck (figs. 81–86)

Female.–Body slender, gradually attenuated behind, with the segments well marked off from each other. Rostrum very short and obtuse, jointed to the head. The hind border of the segments provided with long, slender spines. Caudal rami (fig. 81) nearly twice as long as broad, densely covered with small adpressed bristles. Antennulae (fig. 82) 7-segmented, aesthete much longer than the 3 last segments. Antennae 2-segmented, exopod only one segment, carrying 4 distinctly ciliated setae. P_1 (fig. 83) with small 3-segmented exopod, the whole half as

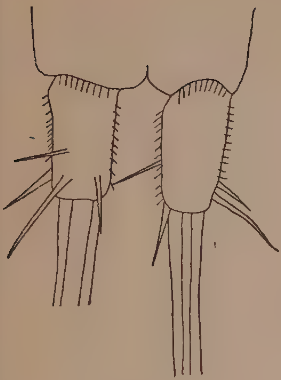

Fig. 81

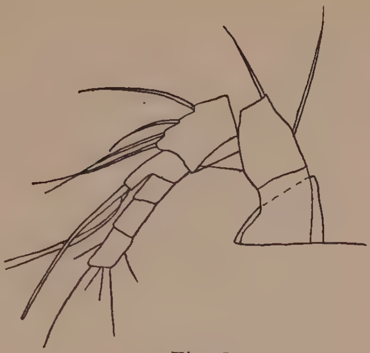

Fig. 82

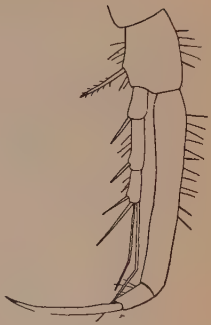

Fig. 83

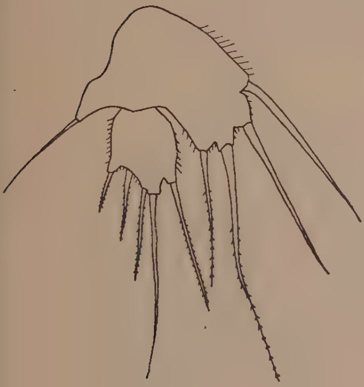

Fig. 84

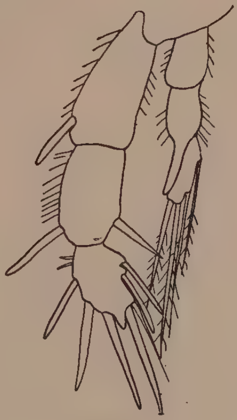

Fig. 85 b

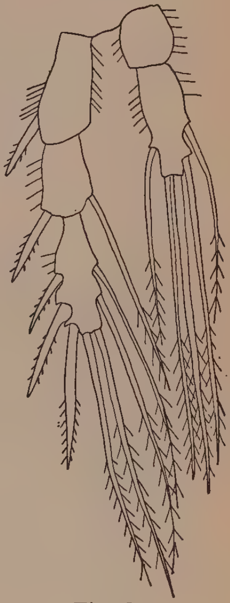

Fig. 85 a

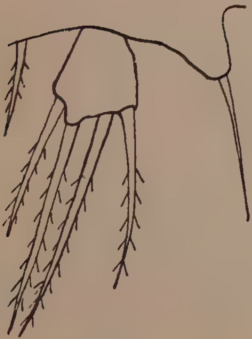

Fig. 86

Figs. 81–86. – *Laophonte curticauda* Boeck

Female: Fig. 81 – Furca. × 370 (Yerseke Bank, 26–VI–1941).
Fig. 82 – Antennula. × 380 (ibid.).
Fig. 83 – P_1. × 250 (ibid.).
Fig. 84 – P_5. × 370 (ibid.).
Fig. 85a – P_3. × 370 (ibid.).
Male: Fig. 85b – P_3. × 290 (ibid.).
Fig. 86 – P_5. × 580 (ibid.).

long as the proximal joint of the 2-segmented endopod and ending with 4 setae diminishing in length from inward to outward boarder. Endopod with a long claw at the tip. P_{2-4} with 2-segmented outer and 3-segmented inner ramus. Last pair of legs: basal part broad and linear, extending nearly as far as the terminal joint, provided with 4 setae, the outermost but one much longer than the others. Terminal part short, oval in form, nearly 1½ times as long as broad (fig. 84).

Male.–Third pair of legs very unlike those of female, (fig. 85 a, b). The outer ramus is very powerful and incurved, with the spines strongly developed and the setae of the inner edge spiniform; endopod 3 articulate, with the middle segment produced to a long process. P_4 likewise somewhat transformed has the outer ramus considerably more strongly built than that of female. Last pair of legs (fig. 86) very small, basal part only a small edge provided with one seta and a prolonged terminal part with 4 setae at the tip.

Length 0.70 mm.

Occurrence: On oysterbeds near Yerseke.

22. *Laophonte elòngata* Boeck (figs. 87–92)

Female.–Body slender and elongated, covered with exceedingly minute hairs, the margin of the abdominal segments provided with mince spinules. Rostrum short and blunt, the furcal joints are nearly nine times as long as broad. Antennulae slender, composed of six joints. Antennae with small, one-segmented outer ramus. The first pair of thoracic feet (fig. 87) are slender, two-segmented exopod much shorter than the two-segmented inner branch, the first joint of the inner branch is elongated, the second very short and armed with a stout terminal claw. The second, third and fourth pairs, which are somewhat similar to each other in structure, with 3-jointed outer rami and two-jointed inner ones, are also slender. The fifth pair (fig. 88) are elongated, basal part armed with 4 setae, terminal joint is linear in shape provided with 5 setae.

Length 0.50 mm.

Male.–Resembling the female in its general appearance, but easily recognizable by the strongly hinged antennulae (fig.89). The fourth joint is dilated and sub-rotund. The terminal joints are narrow and form a claw-like appendage. The third pair of

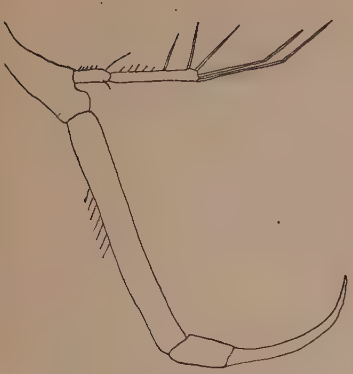

Fig. 87

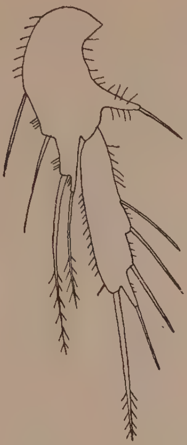

Fig. 88

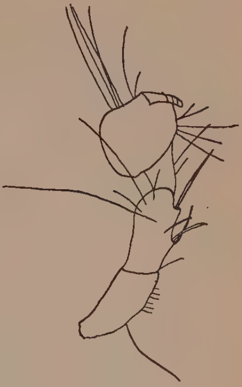

Fig. 89

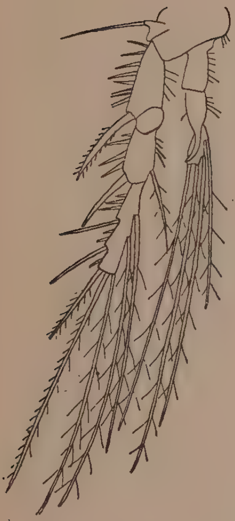

Fig. 90

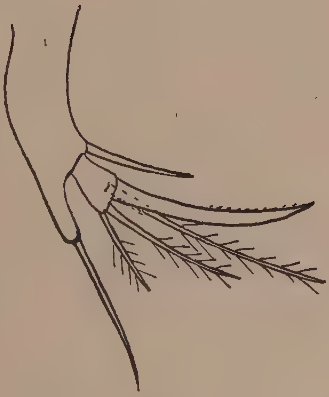

Fig. 91

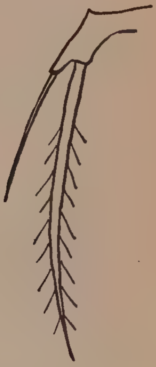

Fig. 92

Figs. 87–92. – *Laophonte elongata* Boeck

Female: Fig. 87 – P_1. × 320 (Oysterpit near Yerseke, 26–X–1942).
Fig. 88 – P_5. × 320 (ibid.).
Male: Fig. 89 – Antennula. × 320 (Oysterpit near Yerseke, 5–X–1942).
Fig. 90 – P_3. × 320 (ibid.).
Fig. 91 – P_5. × 640 (ibid.).
Fig. 92 – P_6. × 640 (ibid.)

thoracic feet (fig. 90) are moderately stout, the inner branch consists of three sub-equal joints that reach to about the second joint of the outer branches. A curved spiniform appendage, extending to the apex of the last joint springs from the end of the second joint. The fifth pair (fig. 91) are very slender, the basal part with one spine, the terminal ending with 3 plumose setae and a strong curved spine. The sixth leg (fig. 92) is very small, furnished with one long plumose spine and a thin hair near the outer border.

Length 0.48 mm.

Occurrence: On oysterpits near Yerseke.

23. *Laophonte minuta* Boeck (fig. 93)

Female.–Body moderately slender, with the segments sharply marked off from each other. Antennulae with seven joints. Antennae with outer ramus rudimentary, ending with two hairs. P_1 outer ramus 3-segmented, much shorter than the first joint of the 2-segmented inner branch. P_2–P_4 with inner branches 2-segmented, much smaller than the exopods. The fifth pair (fig. 93) with the basal part rather broad, scarcely reaching beyond the middle of the terminal part, marginal setae five; terminal part broad oval in form with 6 marginal setae, border provided with denticules.

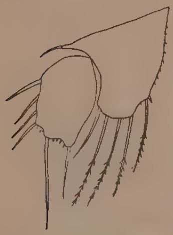
Fig. 93. – *Laophonte minuta* Boeck – Female: P_5. × 500 (Oysterpit near Bergen op Zoom, 6–VIII–1942).

Length 0.80 mm.

Occurrence: Easter Scheldt near Bergen op Zoom in oysterpits.

24. *Asellopsis intermedia* T. Scott

Female.–Body flattened, with Isopod-like shape, all segments lamellarly expanded laterally. Rostrum triangular, not marked off from head. Caudal rami lamelliform, with the apical setae rudimentary. Number of segments of the antennulae reduced. Antennae with 2 segments, exopod one segmented and provided with 3 setae. P_1 both rami 2 segmented with the outer ramus small, endopod strong with very long proximal segment. Rather short distal one ending in a strong claw, basipod and proximal part of exopod set densely with short hairs on the surface. P_{2-4}

exopod 3, endopod biarticulate. Last pair of legs basal and terminal part equal in length first with 4 feathered setae, last with 4 plumose setae and one thin hair. One specimen (♀), not figured.

Occurrence: On oysterbeds near Yerseke.

Fam. CLETODIDAE

25. *Enhydrosoma propinquum* (Brady)

Female.–Body linear in shape, cephalic segment broader than the following segments. Rostral projection broad and blunt. Caudal rami blade-like, provided with 3 setae, the middle one the longer, as long as the ramus itself. Antennulae with 5 joints, short and stout. Antennae with outer ramus well developed, with 2 plumose setae. Thoracic feet with 2 segmented inner branches, last joint the longer, outer branches 3-jointed longer than the inner ones. Last pair of legs with the basal part provided with 3 spines, terminal part elongated, ending with one strong ciliated spine, at the outer margin with 3 plumose spines.

Length 0.57 mm.

Occurrence: One ♀ in an oysterpit near Yerseke, not figured.

Fam. TACHIDIIDAE

26. *Tachidius discipes* Giesbr.

Female.–Body broad, rather flattened. Rostrum conical, small. Segments fringed with fine spines at posterior edge. Operculum prominent with about 12 strong marginal spines. Furcal rami longer than they are broad. Dorsal surface with an oblique row of spines on inner side. Antennulae of 7 segments, antennae of 4, long and slender. Exopod 2-segmented; segment 1 with one seta, last segment with 3. Legs 1–4 similar in form both rami 3–segmented. Leg 5 a broad flat plate, provided with 9 setae.

Length 0.80 mm.

Occurrence: On oysterbeds near Yerseke.

Fam. METIDAE

27. *Metis ignea* Philippi (figs. 94–99)

Female.–Body sub-pyriform in shape with the back more or less curved with no clear demarcation between the anterior and

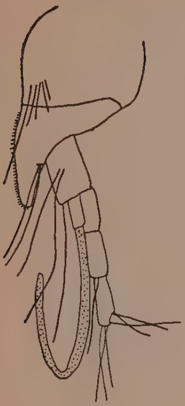

Fig. 94

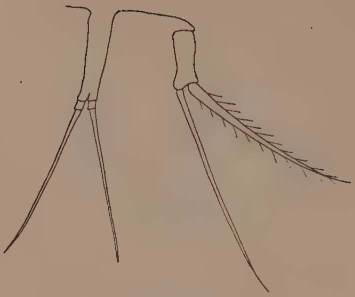

Fig. 96

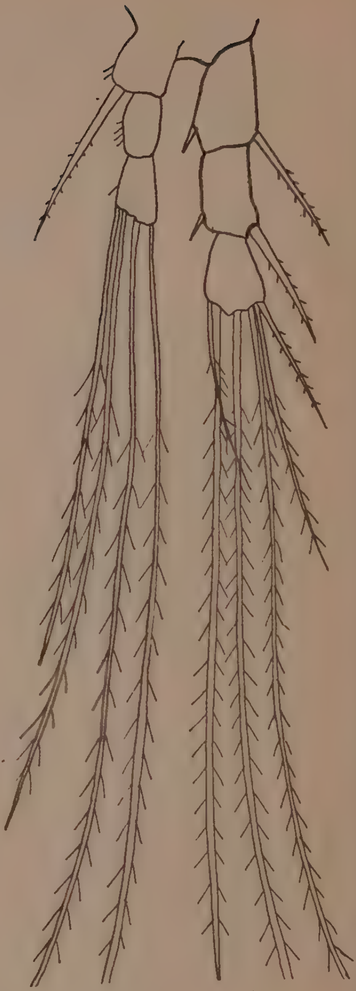

Fig. 98

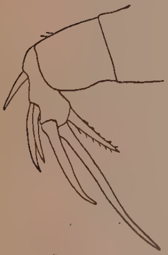

Fig. 95

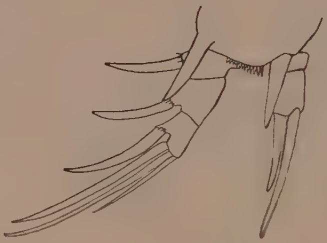

Fig. 97

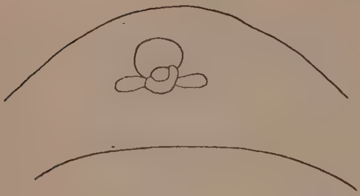

Fig. 99

Figs. 94–99. – *Metis ignea* Philippi

Female: Fig. 94 – Antennula. × 370 (Oysterpit near Yerseke, 4–XII–1941).
Fig. 95 – Antenna. × 250 (ibid.).
Fig. 96 – Oral parts. × 370 (ibid.).
Fig. 97 – P$_1$. × 250 (ibid.).
Fig. 98 – P$_2$. × 500 (ibid.).
Fig. 99 – Genital area. × 370 (ibid.).

posterior division. Cephalic segment very large and vaulted, rostral projection not distinctly defined behind, broad at tip, with 2 slender setae on each side. Urosome rapidly tapered behind. Caudal rami quadrangular, about as long as broad. Eye large and conspicuous. Antennulae (fig. 94) 6-articulate, stout, the 2 proximal joints broad, the second joint with a hook-like projection finely crenulated along the anterior edge, third joint abruptly much narrower than the preceding joints carrying at the end a long aesthete, joints of terminal part subequal in size. Antennae (fig. 95) short and stout, distal joint armed with 6 unequal claw-like spines. Oral parts much reduced (fig. 96) together forming an obtuse cone carrying on each side a bisetose appendage (mandibular palp) and behind a narrow median piece bifurcate at the end (posterior maxillipeds). P_1 (fig. 97) with basal part very thick and massive, carrying at the end a strong spine on each side, exopod 3-articulate somewhat incurved at the base, and without any setae inside, distal joint armed at the tip with 2 strong unequal spines and inside them with 2 slender setae; endopod 2-segmented scarcely half as long as the outer, distal part with 2 strong spines of unequal length at the tip. Legs 2–4 both rami 3-segmented much more slender than the first pair. (fig. 98). Legs 5 imperfectly developed, represented by 2 small juxtaposed lamellae of triangular form and with two very small marginal setae on each lamella. Genital area (fig. 99).

Male.–Somewhat smaller than female. Last pair of legs each produced at end into 2 small digitiform lappets. Colour in preserved state orange, in living species fiery red.

Length 0.55 mm.

Occurrence: On oysterbeds near Yerseke and Bergen op Zoom.

TABLE I. Showing the number of specimens found on 50 Oys

Locality	Oyster-bed 417	Oyster-ground near B.o.Z.	Oysterp								
Date	8-V-41	20-V-41	18-VII-41	24-VII-41	24-VII-41	31-VII-41	31-VII-41	11-VIII-41	11-VIII-41	18-VIII-41	25-
Spatfall	—	—	—	1939	1940	1939	1940	1939	1940	1939	1
Longipedia minor			6♀♀	1♂ 2♀♀		2♂♂ 5♀♀	4♀♀	5♀♀	2♀♀	1♀	4
Ectinosoma melaniceps		1♀									
Harpacticus obscurus		1♀									
Alteutha interrupta			1♂	2♀♀	2♂♂ 1♀		3♀♀	3♂♂	7♂♂ 11♀♀	1♂	
Parategastes sphaericus						1♀					2
Tisbe (Idya) furcata								1♂ 1♀			1
Parathalestris intermedia	41♂♂ 16juvs & ♀♀										
Thalestris longimana											
Amphiascus similis											
Diosaccus tenuicornis											
Ameira parvula											
Mesochra lilljeborgi		1♀									
Nitocra typica											
Asellopsis intermedia											
Laophonte curticauda		2♂♂ 1♀									
Tachidius discipes		1♀									
Metis ignea											

ach of the quantitative samples collected in the year 1941

ar Yerseke

II-	1-IX-41	1-IX-41	10-IX-41	10-IX-41	22-IX-41	22-IX-41	6-X-41	21-X-41	21-X-41	4-XI-41	4-XI-41	4-XII-41	5-XII-41
o	1939	1940	1939	1940	1939	1940	1939	1939	1940	1939	1940	—	—
♀	9♀♀	1♂ 8♀♀	12♀♀	14♀♀	9♀♀	7♀♀	29♀♀	11♀♀	15♀♀	9♀♀	3♀♀	2♀♀	15♀♀
		1♀					2♀♀		8♀♀	1♀			
												1♀	5♀♀
♀	1♀			5♂♂ 2♀♀		1♀							
♀				2♀♀	2♀♀		2♀♀	5♂♂ 15♀♀		2♂♂			1♀
									1♀				1♀
											1♀		
	1♀							1♂		1♀		1♀	1♂ 1♀
										1♀			1♀
					1♀		3♀♀	2♀♀	1♀		1♀	1♀	1♀
			1♀				2♀♀			1♀			
				1♀									
									1♀				
				1♀									
												1♀	1♂

TABLE II. Showing the numbers of specimens found on 50 Oy

Locality	Oysterp										
Date	9/VI	10/VI	16/VI	22/VI	22/VI	30/VI	8/VII	8/VII	15/VII	15/VII	20/
Spatfall	1940	1941	1940	1940	1941	1941	1940	1941	1940	1941	19
Longipedia minor	3♀	3♀	2♂ 33♀ 4 juv.	4♂ 17♀	1♀ 1 juv.	1♂ 5♀	1♂ 4♀	3♂ 15♀	6♂ 5♀	5♂ 14♀	1 3
Ectinosoma gothiceps			1♂ 1♀							1♀	
Ectinosoma melaniceps		1♀		5♀		1♀		2♀		2♀	
Harpacticus obscurus		1♂	2♂ 5♀								
Alteutha interrupta		1♀	1♀				1♀		1♀	1♀	
Parategastes sphaericus	1♀		2♀	1♂						1♂ 2♀	1
Tisbe (Idya) furcata	3♀	7♀	1♂ 16♀							1 juv.	1
Dactylopusia latipes			2♀	7♀	1♀		1♀		3♀		
Dactylopusia micronyx	1♀			1♀			1♀				1
Parathalestris intermedia	1♂										
Thalestris longimana							1♀				
Amphiascus debilis			1♀	2♀							
Amphiascus similis				2♀		1♀	1♀			1♀	
Amphiascus tenellus	2♀	1♀		1♂							1
Diosaccus tenuicornis											
Ameira parvula											
Mesochra pygmea		3♀									
Laophonte curticauda	2♀	1♂ 19♀	2♂ 21♀ 1 juv.	8♀	4♀		3♀	7♀	1♀		
Laophonte elongata											
Laophonte minuta											
Enhydrosoma propinquum											

n each of the quantitative samples collected in the year 1942

near Yerseke

o/VII	28/VII	3/VIII	18/VIII	25/VIII	1/IX	15/IX	22/IX	29/IX	5/X	15/X	26/X		
1941	1941	1941	1941	1941	1941	1941	1941	1941	1941	1941	1941		
18♀ 1 juv.	4♂ 5♀ 2 juv.	3♂ 14♀	13♂ 38♀ 2 juv.	8♂ 15♀	2♀	3♀	1♂ 25♀ 1 juv.	1♀	1♂ 116♀	5♂ 134♀	1♀		
									1♂				
♀			9♀	3♀			1♀		1♂ 64♀	57♀			
											2♂		
♀			6♀		1♀	1♀	2♀	3♀	1♀	1♂ 8♀			
♀		1♀	5♀	1♂ 3♀	2♀	3♂ 1♀	2♂ 8♀	4♀	11♀	5♀	2♀		
♀	1♀		1♀		17♀ 1 juv.			1♀		4♀	14♀		
♂ ♀	1♀												
		1♀											
		1♀											
										44♂ 32♀	10♂ 4♀		
		1♀							1♀				
			1♂ 1♀	1♀			4♀	1♀	9♀	2♀			
							1♀		7♀	2♂ 14♀			
♀				1♀					1♀		1♀		
										2♂ 4♀	2♀		
									1♀				

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THE DEVELOPMENT OF THE EGG OF LIMNAEA STAGNALIS L. FROM OVIPOSITION TILL FIRST CLEAVAGE

BY

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In a recent paper (Raven & Bretschneider 1942), we have published the results of our experiments on the effect of centrifugal force upon the eggs of *Limnaea stagnalis*. They showed that the rate of stratification and the relative proportions of the zones of the stratified egg after centrifugation vary with the stage of operation. This indicated important changes in the physical and chemical composition of the egg protoplasm, occurring during the uncleaved stage of the egg, and made desirable a renewed study of this egg by a variety of methods, in order to elucidate as far as possible its physico-chemical composition at the moment of laying and the processes going on thereafter. Moreover, it was found that a readjustment of the substances displaced by centrifugation takes place at further development. Probably, in this readjustment two different processes are involved: 1. the dispersion of the substances accumulated during centrifuging, leading to an equal or nearly equal distribution of these substances throughout the egg protoplasm, 2. the localisation of particular substances, bringing about the chemo-differentiation of the egg. Though some indications on the occurrence of the last-mentioned process were obtained, definite proof of it can only be given when the localisation of substances during normal development is known sufficiently.

EXTERNAL APPEARANCE OF THE EGGS

The eggs of *Limnaea stagnalis* L. are deposited in the form of large sausage-shaped egg-masses, containing large numbers of eggs. For a description of these masses I may refer to the paper of Nekrassow (1929), giving precise information about their structure and size, the number of eggs and the dimensions of individual egg capsules.[1])

Immediately after the eggs are laid, they are, as a rule, somewhat irregular in outline, flattened or elongated in one direction. After some minutes, however, they round up and become ovoid in form, one of the axes being somewhat shorter than the other; at further development, this proves to be the principal axis of the egg. The dimensions of the eggs are: 117 × 122 μ (average of 42 eggs from 5 egg-masses; the first figure giving the diameter along the egg axis, the second that perpendicular to it). Eggs of different egg-masses may differ somewhat in size, the average diameters varying from 111 × 116 μ to 119 × 130 μ for different masses. The average egg volume, as computed from these figures, is 912000 μ^3.

The egg of *Limnaea* is rather opaque and has a somewhat granular appearance; at first, the yolk granules and yellow pigment are uniformly distributed throughout the egg. Soon, however, a transparent spot appears at one end of the short axis of the egg; this proves to be the animal pole. At this place, the yolk granules and the associated yellow pigment withdraw, leaving a circular area of clear protoplasm. After some time, this area begins to bulge, a conical projection forms and then the first polar body is pinched off. Comandon & de Fonbrune (1935) give good photographic pictures of this process. Immediately after its extrusion, the outline of the egg becomes irregular, pseudopodium-like processes are formed and a considerable deformation of the entire egg may occur, sometimes; in other egg-masses, however, this amoeboid activity is less pronounced. It reaches its maximum 5–10 minutes after the extrusion of the first polar body, then the egg rounds up again.

The time between oviposition and the formation of the first polar body differs very much. It was observed to vary from 120 minutes to 25 minutes at room temperature (± 20° C) in egg-masses, obtained by stimulation of the snails with *Hydrocharis*, as described in our recent paper (Raven & Bretschneider, l.c.)

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[1]) As there exists some confusion in terminology, I will state in advance the terms employed in this paper: egg = the egg cell proper ("Eizelle" Nekrassow, "vitellus" Crabb 1931); egg capsule = "Ei" Nekrassow = "egg" Crabb; it consists of the egg cell with the surrounding albuminous fluid, enveloped by a double membrane; egg-mass = the egg capsules together (= "Laich" Nekrassow), embedded in a common jelly mass and surrounded by a rather firm envelope ("Kapselhülle" Nekrassow).

On an average, the first polar body may be extruded about 60–70 minutes after the eggs are laid. The differences in the time between oviposition and first polar body may be explained by the fact that the insemination of the eggs takes place in the oviduct of the adult; therefore, development begins before the eggs are laid, during their passage through the female ducts and the formation of the egg-mass. Probably, the time between insemination and oviposition may vary considerably, and in consequence of this the eggs may be laid at different times before the first maturation division.

The second polar body is formed about one hour after the first; its extrusion is accompanied again with a phase of amoeboid activity. The deformation of the egg reaches its maximum about 10 minutes after the extrusion of the polar body, then the activity diminishes and the outline of the egg becomes regular again.

At this stage, a fine membrane, enveloping the egg, can be observed. The position of the polar bodies with respect to this membrane is very remarkable; the first polar body lies outside the membrane, the second polar body is situated inside (fig. 1 g). It may be concluded that at the moment of first polar body formation this membrane has not yet been formed, or has such a consistency that it is pierced easily by this polar body; between first and second polar body, it is formed or its consistency changes, so that it is impenetrable at the time the second polar body is extruded.

About 100–110 minutes after the extrusion of the second polar body, the egg begins to elongate perpendicularly to the egg axis. The first cleavage groove appears at the animal side of the egg about 120–130 minutes after the formation of the second polar body (at ± 20° C).

NUCLEAR PHENOMENA DURING MATURATION AND FERTILIZATION

In eggs of *Limnaea stagnalis* fixed immediately after oviposition, the germinal vesicle has, as a rule, broken down. The maturation spindle occupies the axial part of the egg; one of its end is situated at a little distance under the surface at the animal pole, the other end lies near the centre of the egg. At both ends of the spindle, a moderate aster is formed (fig. 1 a, 2). In the spindle equator the tetrads are lying. In the egg protoplasm, the spermatozoön is found. The sperm-head, a rather large compact dark body, lies immediately beneath the egg cortex; it may be surrounded by a clear area, having the appearance of a vacuole, as was described already by LINVILLE (1900). In some early cases, it is still attached to the tail, which forms a coiled thread in the egg protoplasm; soon, however, it breaks away from the tail, which is resorbed in the cytoplasm. In some exceptional cases two sperm-heads were observed in one egg, both having a subcortical position. Never, however, could several sperm-heads in the inner egg protoplasm, as described by CRABB (1927) in *Limnaea stagnalis appressa* Say, be discerned with any amount of certainty. As a matter of fact, my observations differ in many respects from the relations described by CRABB in that form; for this difference I can give no explanation, unless it might be supposed that under the influence of the isolation of "virgin" individuals and the resulting self-fertilization in CRABB's experiments the fertilization process shows many abnormalities. On the other hand, my observations are in many respects entirely in accordance to those of KOSTANECKI & WIERZEJSKI (1896) om *Physa*, of LINVILLE (1900) on *Limax* and *Limnaea* and of E. F. BYRNES (1900) on *Limax*.

During the first part of the anaphase stage of the first maturation division, no considerable change in the situation of the maturation spindle occurs. However, at a late anaphase stage, the outer end of this spindle comes into contact with the egg surface at the animal pole; at this place, a pit-like depression of the surface appears. The aster at this end of the spindle flattens against the egg surface, its radiations extending somewhat into the egg protoplasm; the aster at the opposite end has not changed (fig. 1 b, 3).

Ten minutes later, the formation of the first polar body begins. The peripheral end of the maturation spindle retains its contact with the egg surface at the top of the conical projection bulging at the animal pole(cf. RAVEN & BRETSCHNEIDER 1942, Pl. VI). The astral rays at this end disappear more and more as the expulsion of the polar body progresses. The aster at the inner end of the maturation spindle, on the contrary, has grown very large, occupying a large part of the animal half of the egg (fig. 1 c); it contains a large clear "central body", which represents, probably, the liquefied area in the centre of the gelated aster. At the time the dyads have reached the spindle poles the first polar body is pinched off.

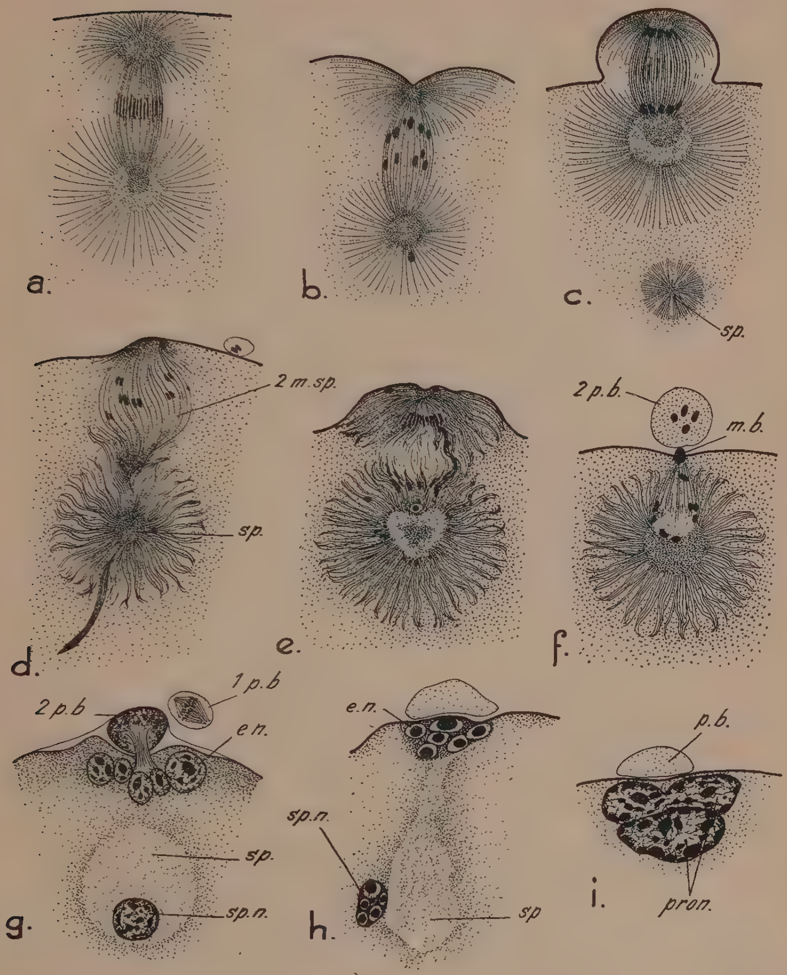

Fig. 1. Maturation and fertilization in *Limnaea*. *a*. 1st maturation spindle, early anaphase. *b*. Late anaphase. Spindle end in contact with egg cortex. *c*. Telophase. Formation of 1st polar body. Spermaster (sp) just formed. *d*. 2d Maturation spindle (2.m.sp.). Expansion of spermaster. *e*. Late anaphase. *f*. 2d polar body (2.p.b.) formed. Spindle remnant and mid-body (m.b.). *g*. Karyomeres of egg nucleus (e.n.) in subcortical plasm. Sperm nucleus (sp.n.) in central area of spermaster (sp.). *h*. Spermaster (sp.) in connection with animal pole. *i*. Copulation of pronuclei (pron.).

In this phase, it was tried to determine the number of dyads in the maturation spindle and first polar body. From repeated counts in different eggs resulted a number of about 16–18 dyads. This corresponds rather well to the (haploid) chromosome numbers given by Perrot (1938), being 16 for *Limnaea elodes* and 18 for *Limnaea stagnalis* var. *Rhodani*. Crabb (1927) gives a haploid number of 10 for *Limnaea stagnalis appressa* Say, however.

Shortly before the extrusion of the first polar body, the spermaster makes its appearance (fig. 1 c). In one case it has been observed that the aster was situated at one of the ends of the coiled threadlike sperm, which, however, did not reach the centre of the spermaster, but ended at its periphery (fig. 1 d). At first, the spermaster is a small structure lying near the centre of the egg, at some distance from the deep pole of the maturation spindle. It contains no "central body", the astral rays meeting in one point at the centre of the spermaster (fig. 1 c). During the formation of the second maturation spindle, it grows somewhat in diameter, retaining its central position in the egg; at the same time, a small "central body" appears. Meanwhile, the sperm-head retains its subcortical position. This spacial separation between sperm-head and spermaster has been clearly recognized already by Kostanecki & Wierzejski (1896).

The second maturation spindle is shorter than the first, and lies nearer the surface of the egg; the asters at its ends are at first rather inconspicuous (fig. 1 d), then they grow rapidly, especially the deep aster. No spiral asters were seen, neither in this nor in the first maturation division (cf. Weigmann 1928). At the anaphase of the second maturation division, the egg surface at the peripheral end of the spindle begins to bulge (fig. 1 e). The extrusion of the second polar body is accompanied with the same phenomena as that of the first. The second polar body remains often connected with the egg for a considerable time; a spindle remnant and associated "mid-body" (cf. Fry 1937) may be found until one hour after its formation (fig. 1 f, g).

Directly after the completion of the second maturation division, the chromosomes of the egg nucleus swell into little vesicles, containing each a dark granule; 18 of such karyomeres could be counted in one case. They lie in a large clear area in the centre of the inner aster of the maturation spindle which occupies the animal part of the egg. In the course of the first hour after the extrusion of the second polar body, this aster grows considerably, then it vanishes. After its disappearance the karyomeres of the egg nucleus are lying in the subcortical protoplasm at the animal pole of the egg (fig. 1 g).

The spermaster, which appeared during the first maturation division, has at the time of second polar body formation attained a stage, in which a central area of clear, highly vacuolated protoplasm is surrounded by a zone of denser protoplasm, in which the astral rays are no longer very conspicuous. A division of the spermaster or its transformation into an amphiaster has not been observed in my preparations, neither in this nor in preceding stages. Shortly after the extrusion of the second polar body, the sperm-head, which has remained inactive till this moment, leaves its subcortical position and moves to the spermaster, where it comes to lie in the central clear area (fig. 1 g). This migration of the sperm-head progresses rather quickly; no intermediate phases of it have been observed. At the same time, the sperm-head becomes vacuolated and develops into the male pronucleus.

TABLE I

	Egg nucleus	Sperm nucleus	Spermaster
60 min. before 1st p.b.	1st Maturation spindle, metaphase.	Subcortical sperm-head.	
30 ,, ,, 1st ,,	End of mat. sp. reaches egg cortex	,, ,,	
20 ,, ,, 1st ,,	Anaphase of 1st mat. division.	,, ,,	
Extrusion of 1st p.b.	Telophase of 1st mat. div. Central aster large.	,, ,,	small
40 min. before 2d p.b.	2d mat. spindle, metaphase.	,, ,,	growing
20 ,, ,, 2d ,,	Anaphase of 2d mat. division.	,, ,,	,,
Extrusion of 2d p.b.	Telophase of 2d mat. div. Central aster large.	,, ,,	,,
20 min. after 2d p.b.	Karyomeres in large aster.	♂ pronucleus moves to spermaster.	Spermaster with clear central area
60 ,, ,, 2d ,,	Karyomeres at anim. pole under cortex.	♂ pronucleus in spermaster	,, ,,
40 min. before 1st cleav.	Pronuclei united		Spermaster disappears.
20 ,, ,, 1st ,,	Cleavage spindle, metaphase.		

In the second hour after the completion of maturation, the spermaster moves to the animal pole of the egg; the dense protoplasm surrounding it gets into contact with the animal pole plasm, in which the karyomeres of the egg nucleus are lying. In one case it has been observed that the clear area of the spermaster extended in the form of a neck-like projection unto the animal pole (fig. 1h, 4). Then, the male pronucleus moves to the animal pole, where it meets the female pronucleus. The remnant of the spermaster vanishes altogether. Both pronuclei may consist, at this moment, of a number of vesiculous karyomeres; progressively, however, these karyomeres fuse. Owing to this origin, the pronuclei have a rather irregular outline, at first (fig. 1 i). At this time, they have reached the prophase stage. Then, about 20 minutes later, the nuclear membranes are lost and the cleavage spindle makes its appearance.

Table I gives the time relations of these phenomena.

CYTOPLASMIC COMPONENTS OF THE EGG

In centrifuged eggs of *Limnaea stagnalis* (RAVEN & BRETSCHNEIDER 1942), 3 types of granules could be discerned: α-granules (probably mitochondria), accumulating in the 3d zone of the egg; β-granules, forming the major part of the albuminous yolk and heaped up in the 4th zone at the centrifugal end of the egg; and γ-granules, the largest of the three, probably representing a particular element connected with the formation of vacuoles in the cytoplasm. In eggs centrifuged before maturation, these last-mentioned granules are accumulated at the heavy pole of the egg; when the formation of vacuoles has begun, they become progressively lighter and are displaced upon centrifugation to the light pole.

The distribution of these inclusions and of other cytoplasmic components of the egg was studied in normal eggs, fixed at various moments during the uncleaved stage in Bouin or Zenker and stained with iron haematoxylin and eosin, with azan or after Dominici. Especially the azan-stained sections gave very instructive pictures of the composition of the egg.

In eggs fixed immediately after laying, two major portions of the cytoplasm can be distinguished (fig. 2). At the vegetative pole, a special plasm is situated, staining blue with azan; in a meridional section, it covers a sector of about 110° having its top near the centre of the egg. In view of its ultimate position, we will call it the ectoplasm. The rest of the egg consists of endoplasm, being orange-red in azan-stained sections; only

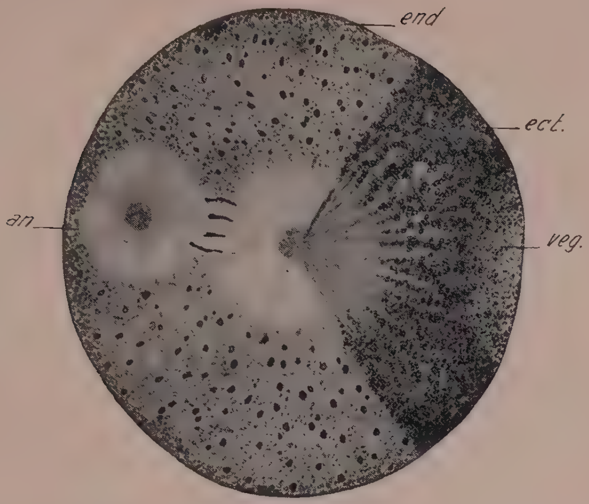

Fig. 2. Egg of *Limnaea stagnalis*, immediately after laying (FT-I). Early anaphase of 1st maturation division. Ectoplasm (ect.) forms sector at vegetative pole (veg) of egg. Sectorial coloration of deep maturation aster. an = animal pole, end = endoplasm.

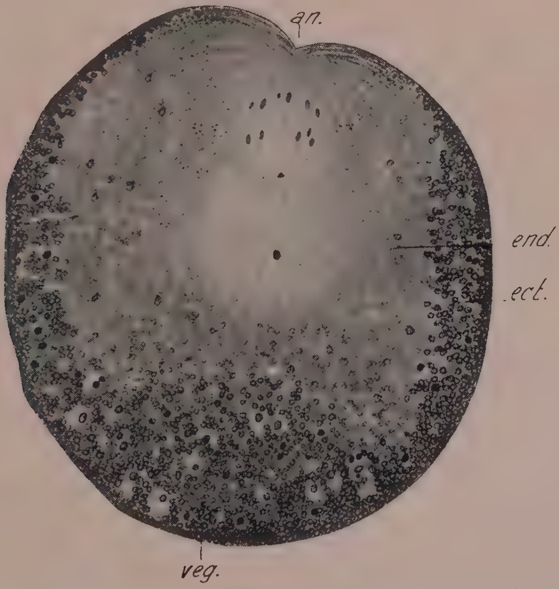

Fig. 3 Late anaphase of 1st maturation division (FU-I). Peripheral spindle end in contact with egg cortex at animal pole (an); depression of egg surface. Ectoplasm (ect) has spread beneath egg cortex and surrounds endoplasm (end), except at animal side.

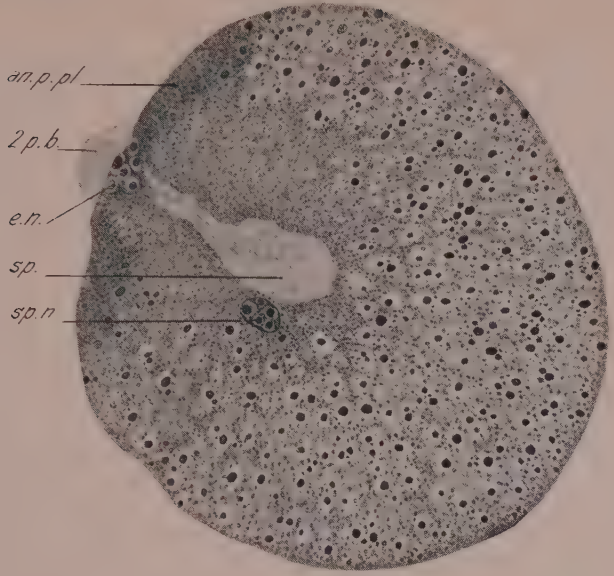

Fig. 4. Normal egg of *Limnaea stagnalis*, about one hour before cleavage (AS-IV). Animal pole plasm (an.p.pl.) at animal side beneath egg cortex; rest of protoplasm vacuolated, γ-granules in vacuoles. Spermaster (sp) with clear area, reaches with neck-like projection unto animal pole, where karyomeres of egg nucleus (e.n.) are lying.

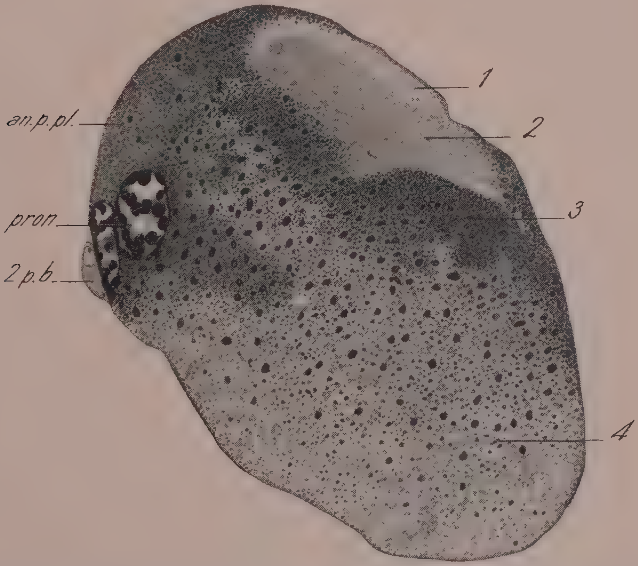

Fig. 5. Egg of *Limnaea stagnalis*, centrifuged just after laying and fixed 3½ hours later (AO-IV). 1–4 Layers of stratified egg substances; readjustment not very complete in this case. Animal pole plasm (an.p.pl.) accumulated in neighbourhood of animal pole, where pronuclei (pron) are lying.

in the equatorial part of the egg, some dispersed patches of blue ectoplasm may be found in the outer layer of the egg, immediately under the vitelline membrane.

The ectoplasm contains a dense mass of albuminous yolk; as a matter of fact, the greater part of the β-granules are accumulated in this plasm. They stain dark indigo blue with azan. At the vegetative pole of the egg is a small cap of finer granules, staining light greyish blue. The endoplasm, on the other hand, though it contains a few scattered blue β-granules, is rather characterized by its riches in α- and γ-granules. Both are red, but, whereas the large γ-granules have a deep red color, the finer α-granules show an orange-red tint. A few γ-granules may be found also, scattered between the β-granules in the ectoplasm.

It might be supposed that the difference between the ectoplasm and endoplasm is brought about by the local accumulation of the granular inclusions only, but that it does not involve the intergranular "ground-plasm" of the egg. Some observations seem to prove, however, that this is not the case. The astral rays of the maturation asters always show the same color as the plasm in which they are embedded. Most remarkable pictures arise, when one of the asters is situated at the boundary between ecto- and endoplasm, which is at this stage a rather common occurrence: that part of the aster that is situated within the ectoplasm sector is blue; the rest is orange-red (fig. 2). This fact was noted already in our centrifuged eggs, where asters at the boundary of the blue and red zones showed the same sectorial color difference. As we may take for granted that the astral rays arise by a gelification of the hyaloplasm, this observation points to the conclusion that not only the granular inclusions, but also the intergranular hyaloplasm in the ectoplasmic and endoplasmic regions differs in its physicochemical composition. The objection that this sectorial coloration of the aster might be an artifact, arising during staining by a transfer of stained substance from the heavily stained yolk granules to the astral rays in the immediate vicinity, is refuted by the observation that these rays show an even coloration from the periphery of the aster, where they penetrate somewhat between the granules, unto its centre, and that the line of demarcation between the differently colored parts of the egg is within the aster as sharp as it is elsewhere.

Furthermore, our sections of centrifuged eggs stained with azan seem to show that upon centrifuging the ectoplasm can be displaced as a whole to the centrifugal end of the egg. This is not the case with the endoplasm, which is separated by centrifugal force into its components, the hyaloplasm, α-granules and γ-granules each accumulating in different zones of the stratified egg.

The relative positions of the ectoplasm and endoplasm, as found immediately after laying, do not remain the same. The ectoplasm begins to spread beneath the egg cortex to the animal side of the egg. Fig. 3 shows the situation as it is shortly before the extrusion of the 1st polar body. The ectoplasm covers the vegetative hemisphere and the sides of the egg, leaving free a rather wide area around the animal pole. At the vegetative pole it projects with a knob-like prominence into the interior of the egg, at the sides it forms a rather thick layer narrowing to the animal side, where it ends in a sharp edge. The endoplasm composes the remaining part of the egg and surrounds the maturation spindle.

In the next hour, the ectoplasm spreads more evenly around the egg and the knob-like accumulation at the vegetative pole disappears. Still, this layer is thicker at the vegetative side and diminishes gradually unto the animal side, where a gap remains till after the completion of the 2d maturation division. Then this gap is filled, the ectoplasm now surrounding the whole egg.

About one hour before the first cleavage, at the animal side of the egg a new cytoplasmic differentiation becomes visible: the animal pole plasm (fig. 4). It is a layer of very dense protoplasm, lying immediately beneath the egg cortex in the animal hemisphere, and staining dark violet blue with iron haematoxylin. Contrary to the rest of the cytoplasm, it contains no vacuoles; many α-granules, however, are accumulated in this plasm. As to its origin, the following observation is of interest: In eggs centrifuged before maturation, one hour before cleavage an animal pole plasm may be formed under the cortex at the original animal side of the egg, irrespective of the stratification of substances (fig. 5). It seems, therefore, that its formation is determined by an attraction, exercised by a particular region of the egg cortex upon some substance distributed through the cytoplasm, in the same way as it was shown by LEHMANN (1940) for the pole plasms of *Tubifex*. On the other hand, there is some indication that the pole plasm has something to do with the vanishing maturation aster. After the extrusion of the 2d polar body, this aster continues to grow, until (about 40 minutes later) it occupies a large part of the animal hemisphere. At the same time, the astral radiations begin to become less distinct; ultimately, they become inconspicuous altogether. Meanwhile, the polar plasm has developed; at first it occupies about the same area as the aster did before, then it condenses into a rather narrow subcortical layer at the animal pole. Perhaps, the centripetal flow of protoplasm to the centre of the dilating aster aids in the transportation of the pole plasm substance to the animal pole. The behaviour of the α-granules is suggestive in this respect: they gather around the maturation asters (fig. 3), then they may be seen in the sections to be arranged in rows between the astral rays of the dilating aster; finally, they are found in the animal pole plasm.

A word remains to be said about the development of the vacuoles of the egg. In eggs recently laid, no vacuoles are present in the cytoplasm. Large γ-granules are found both in ecto- and endoplasm, but in the endoplasm their number is much greater (fig.2). During the maturation divisions, they have a tendency to gather around the spindle and asters, forming, together with the α-granules, a dark halo surrounding the mitotic figure. After the completion of the maturation divisions, however, they spread more evenly through the egg, contrary to the α-granules, which accumulate in the pole plasm. About 10 minutes before the extrusion of the 1st polar body, a narrow vacuolar space may be seen surrounding some of the γ-granules (fig.3). In the next hours, these vacuoles surrounding the γ-granules increase both in number and in size, until shortly before the 1st cleavage the cytoplasm has a vacuolar appearance throughout, with the exception of the animal pole plasm, which is more compact; at the same time, all the γ-granules of the egg lie within a vacuole (fig. 4). As in our former paper (RAVEN & BRETSCHNEIDER l.c.) we have to conclude, therefore, that the vacuoles of the egg arise from the γ-granules, which attract water from the neighbouring protoplasm and are, in that way, surrounded by a mantle of fluid.

The Golgi bodies of the egg are distributed rather evenly through the cytoplasm, leaving free only the spindle and asters at the animal side of the egg. This distribution was observed already by GATENBY (1919). After the formation of the vacuoles, the

Golgi bodies lie in the cytoplasmic meshes between the latter, together with the α-granules (mitochondria), the β- (albumen) granules and the fat droplets (cf. below p. 115). After treatment with silver nitrate, the Golgi bodies are partly impregnated as a whole, probably representing the praesubstance of Hirsch (1939); partly, they form black rings or horseshoes, surrounding a lighter or colorless "internum" ("Golgi systems", Hirsch).

The movements of the egg substances in the eggs of *Limnaea columella* and some other pulmonates, as they may be seen in the living eggs, were described by Conklin (1910). After the dissolution of the germinal vesicle a clear area, containing the maturation spindle, comes into contact with the surface at the animal pole of the egg; then, a deep "well" of clear protoplasm leads down to the centre of the egg. It is surrounded by a finely granular substance which is distinct from the yolk and the clear protoplasm. During the maturation divisions, the clear protoplasm is spread out on the surface as a cap at the animal pole; after the second maturation division, it begins to spread over the upper hemisphere, and at the time of the first cleavage it has reached the equator of the egg. The advancing edge of the cap becomes thickened. The pronuclei meet at the animal pole, where they lie in a deeper portion of the clear protoplasm; immediately beneath these nuclei is a layer of finely granular yellow substance, which later surrounds the nuclei and the cleavage spindle.

In this description, the "well" of clear protoplasm at the animal pole represents, evidently, the area of the maturation spindle and asters which is free of granules. The finely granular yellow substance is the mass of α-granules, surrounding the maturation spindle, later accumulating in the animal pole plasm. The "spreading" of the clear substance over the animal hemisphere corresponds to the formation of the animal pole plasm. As a matter of fact, however, the order of events is interpreted rather incorrectly. The study of sectioned eggs has shown that no movement of protoplasm from the animal pole to the equator can be detected; on the contrary, the direction of movement is quite the reverse, the ectoplasm spreading subcortically from the vegetative unto the animal pole. Evidently, the study of whole eggs does not give a true picture of the processes occurring in this stage of development.

PHYSICAL CHANGES IN THE EGG

1. Increase in volume: As noted above, the diameter of the eggs immediately after oviposition is, on an average, 117 × 122 μ, the egg volume = 912000 μ^3. It was observed, however, that the egg diameter increases considerably up to the time of first cleavage. Therefore, some batches of eggs were measured at regular intervals from the time of laying till first cleavage. Fig. 6 shows the results of one of these experiments.

Egg-mass JE. 12 Eggs were chosen for the experiment. First measurement immediately after oviposition, 1 hour before extrusion of first polar body: Average diameter 119 × 130 μ, average volume = 1058000 μ^3. In the next hour, the size of the eggs increases at first slowly, then more rapidly. 5 Minutes after the extrusion of the first polar body, the average diameter is = 122 × 140 μ, the average volume = 1246000 μ^3. The rapid rise in diameter at the time of polar body formation is followed by a standstill, perhaps even a decrease in diameter in the next 20 minutes; then the swelling of the egg slowly continues, to show again an acceleration at the time of extrusion of the second polar body. From this moment on, the increase is again more slowly, to reach a third maximum about one hour before first cleavage. At this time, the average diameter amounts to 137 × 142 μ, the average volume to 1440000 μ^3. Again, a decrease occurs, then the graph shows a rapid rise; in this period, however, the elongation of the egg preceding cleavage makes a precise determination of the egg volume difficult; it is not certain, therefore, that this rise is significant.

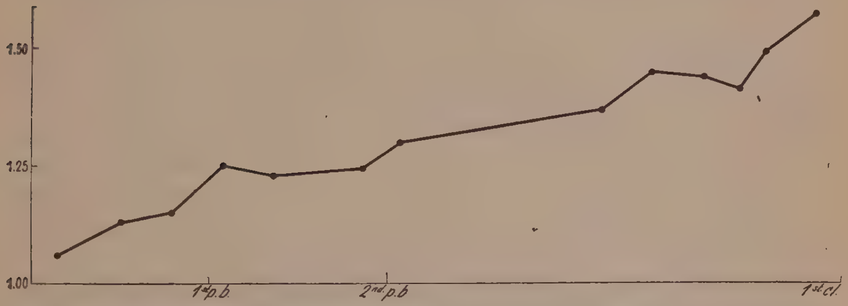

Fig. 6. Graph showing increase in volume from oviposition till 1st cleavage (average of 12 eggs, experiment JE). Abscissae: time. Ordinates: volume in $10^6\ \mu^3$.

From the time of laying till one hour before first cleavage, i.e. in about 4 hours, the egg volume in this case showed an increase of 36%. In another case, in which the rate of development had increased in consequence of a higher room-temperature, an enlargement of 45% in 175 minutes was observed; in still other egg portions, increases of 51% and 40% in 3½ hours were measured.

Furthermore, the measurements show that development is accompanied with small, but distinct changes in form of the egg. The flattening at right angles to the egg axis is most distinct immediately after the extrusion of either of the polar bodies, the quotient (diameter along egg axis : transverse diameter) may reach a value as low as 0.75 at this time. Between both maturation divisions the egg becomes more nearly spherical, the above-named quotient amounting to an average of about 0.97; after the second maturation division, the egg again gradually becomes more spherical, the quotient obtaining a value of about 0.99 shortly before the first cleavage.

Clement (1938) observed an average increase in volume of 29% resp. 38% in eggs of *Physa heterostropha*. As the first measurements were made by him after the first polar body was extruded, it is not surprising that his figures are somewhat lower than ours; in general, however, we may say that the increase in volume in *Physa* is of the same order of magnitude as that in *Limnaea*.

Apparently, this swelling of the egg is brought about by an absorption of substances, especially water, from the surrounding fluid filling the egg capsule. Clement has connected it with the formation of vacuoles in the egg protoplasm by a swelling of coarse unpigmented granules. As we will see, this interpretation is, probably, correct.

2. Specific gravity: the absorption of water by the egg will, presumably, diminish its specific gravity. Comandon & de Fonbrune (1935) have observed fluctuations in density in the eggs of *Limnaea limosa*. At first, the egg is heavier than the surrounding egg capsule fluid and rests at the bottom of its capsule; its density diminishes gradually and at the time of second polar body formation it equals that of the fluid; then, the egg becomes lighter and rises to the highest point of the capsule. These fluctuations were ascribed by the authors to an absorption of fluid by the egg. If we compare their fig. 5 with fig. 6 of this paper, it becomes evident that there exists a complete parallelism between the changes in density of the egg in *L. limosa* and the rate of intake of fluid in *L. stagnalis;* in both figures, the graph shows distinct maxima at corresponding places (1st polar body, 2d polar body, half way between this and 1st cleavage). In *Limnaea stagnalis*, the egg capsule fluid has a high viscosity; therefore, the displacements of the egg as a result of changes in density are not distinct; however, very slow displace-

ments corresponding to those in *Limnaea limosa* could be observed by COMANDON & DE FONBRUNE in this form, too. Some measurements, which were made by me, gave a full confirmation of their results; at first, the egg falls slowly; after the extrusion of the second polar body, there is a slow rising movement; in either case, the rate of displacement does not exceed 4 μ per minute.

3. Viscosity: The viscosity changes of the egg protoplasm were studied by means of the centrifugation method. Egg samples were centrifuged at different moments between oviposition and first cleavage during 5 minutes at a velocity of 3800 revolutions per minute, giving a centrifugal pressure of 1860 × gravity. The degree of stratification brought about by this treatment was used as a means to estimate relative viscosity changes. Viscosity is low if the eggs are fully stratified, it is relatively high if stratification is less distinct. As the number of eggs of one egg-mass was insufficient for an entire experiment, three or four egg-masses were used; preliminary experiments showed that the differences between individual egg-masses are insignificant. The time, at which the eggs were centrifuged, was related to the developmental processes as observed in control eggs of the same batch: extrusion of first and second polar body, first cleavage. The temperature was kept at 20° ± 0.5° C. Immediately after the eggs were taken from the centrifuge, they were examined by means of a horizontal microscope; as the eggs orient rapidly with their heavy yolk pole down, in this way most or all eggs are looked upon at right angles to the axis of centrifuging, and the degree of stratification can be determined easily. As a rule, this is nearly equal in all eggs. One of the eggs, showing the average condition of the sample, was brought into focus and photographed exactly 5 minutes after the end of centrifugation. Fig. 7 shows a series of pictures obtained in this way.

The first of these eggs (7^1) was centrifuged shortly after laying, 27 minutes before the extrusion of the first polar body (in all instances, the time is given at which centrifugation ended). Stratification is distinct; the four zones described in our former paper (RAVEN & BRETSCHNEIDER 1942) can be observed readily. There is a rather sharp line of demarcation between zone 1 (fat) and 2 (hyaloplasm) and between zone 3 (α-granules) and 4 (β-granules); between zones 2 and 3, the demarcation is more vague. In the hyaloplasm zone, the maturation spindle and asters are indicated as a somewhat opaque elliptical band; for the rest, this zone is very transparent and contains no granulations. Fig. 7^2, 18 minutes before 1st polar body, shows the same relations. In 7^3, however, centrifuged ± 5 minutes before the extrusion of the first polar body, which was well under way at the time the photo was

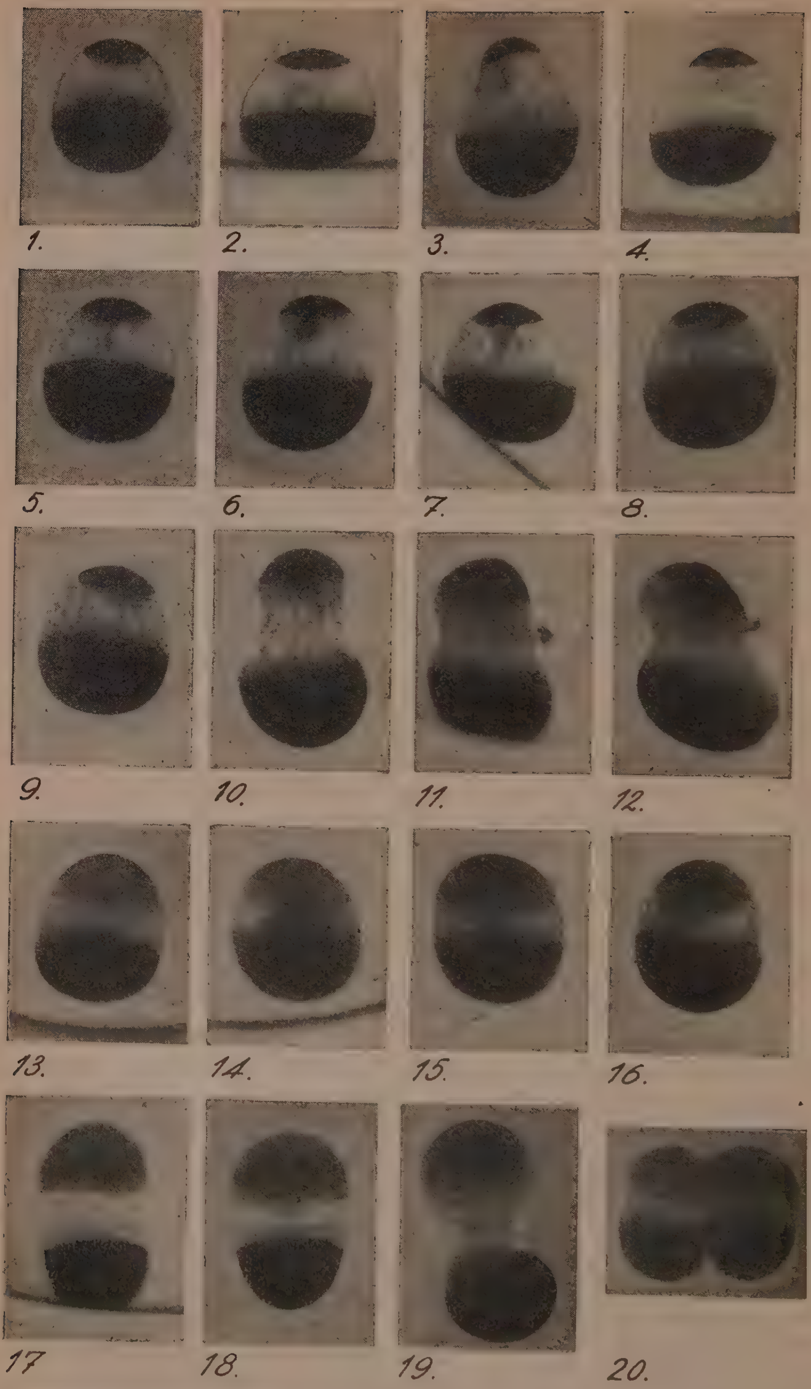

Fig. 7. Effect of centrifugation (5 min., 3800 revol./min) at different moments during uncleaved stage of egg, 1. 27 min., 2. 18 min., 3. 8 min. before 1st polar body, 4. 13 min., 5. 12 min., 6. 25 min. after 1st polar body, 7. 25 min., 8. 11 min. before 2d polar body, 9. 3 min., 10. 16 min., 11. 33 min., 12. 48 min. after 2d polar body, 13. 68 min., 14. 69 min., 15. 50 min., 16. 35 min., 17. 36 min., 18. 20 min., 19. 5 min. before 1st cleavage, 20. 10 min. after 1st cleavage.

taken, small droplets have appeared in the hyaloplasm zone. Probably, these are the vacuoles formed by swelling of γ-granules, and thereby becoming lighter, so that they accumulate in more centripetal parts of the egg, as observed in our former paper. For the rest, the demarcation of the layers is distinct, indicating that the viscosity of the egg has not changed considerably. In 7^3, the vacuoles are most numerous in zone 3 and the adjacent parts of zone 2, but in the next figures the vacuoles gradually invade the whole of zone 2 (cf. fig. 7, $^{4-7}$); then, they accumulate at the boundary of zone 1 (fig. 7, $^{10-11}$) and fuse with this zone into a common mass (fig. 7, $^{12-13}$). Meanwhile, the degree of stratification has changed. Beginning with the egg of fig. $7,^8$, centrifuged 11 minutes before the extrusion of the second polar body, the zone of hyaloplasm has become narrower, the demarcation of the zones is less distinct; apparently, viscosity is increasing. This rise in viscosity continues until the stage of fig. $7,^{14}$, (69 minutes before 1st cleavage), when it reaches its maximum. At this time, the hyaloplasm zone is very narrow and the demarcation to the adjacent zones is vague. Nineteen minutes later (fig. 7^{15}), the egg is somewhat more stratified again; evidently, the viscosity is somewhat less. In the next 14 minutes, the viscosity drops rapidly; the egg of fig. 7^{17}, centrifuged 36 minutes before the 1st cleavage, is fully stratified again. Then there is again a gradual rise in viscosity (fig. $7,^{18}$, 20 minutes before 1st cleavage). In fig. 7^{19}, centrifuged 5 minutes before the beginning of cleavage furrows, stratification is medium to low, indicating a relatively high viscosity; the same holds true for fig. 7^{20}, centrifuged 10 minutes after the beginning of cleavage.

The results indicate a regular series of viscosity changes during the uncleaved stage of the egg. Immediately after laying, viscosity is low; it remains so during the first maturation division, begins to rise shortly before the extrusion of the second polar body, reaches a maximum about half way between second maturation and first cleavage, then drops rapidly, has a minimum half an hour before cleavage, and rises again until cleavage (fig. 8).

If we relate these viscosity changes to the processes going on in the egg, it appears that the first rise in viscosity corresponds in time to the growth of the spermaster; the drop of viscosity to the fusion of the pronuclei and the preparation of the cleavage spindle; and the second rise to the cleavage mitosis.

Fry & Parks (1934) studied the viscosity changes in the eggs of *Arbacia*, *Cumingia* and *Nereis*. They found as many cycles of change in viscosity as there are mitotic cycles. Maxima of viscosity corresponded not only to the fusion of the pronuclei and the first cleavage division, but (in *Cumingia* and *Nereis*) to the formation of either of the polar bodies as well. Viscosity was low at the beginning of a mitotic cycle, rising whenever the cell processes are in action and high at the end of a mitotic cycle.

Similar viscosity changes were observed by LEHMANN (1938) in the eggs of *Tubifex*, though the time schedule of these changes does not fully agree in both cases.

In *Limnaea*, on the contrary, the number of cycles of change in viscosity does not correspond to the number of mitotic cycles. During the maturation divisions, viscosity shows no significant cyclic changes; only during the last part of the uncleaved stage the viscosity changes agree with those in *Arbacia*, *Cumingia* and *Nereis:* a maximum of viscosity when the spermaster is at its height, a rapid drop to a minimum at the prophase of first cleavage, and a rise when cleavage mitosis is in action.

4. Tension at the surface: When *Limnaea* eggs are centrifuged at 3800 revolutions per minute, they elongate under the influence of the centrifugal force; they cannot, however, in 5 minutes be pulled apart with this force. The degree of elongation, brought about in this way at different moments during the uncleaved stage can be used for the evaluation of the "tension

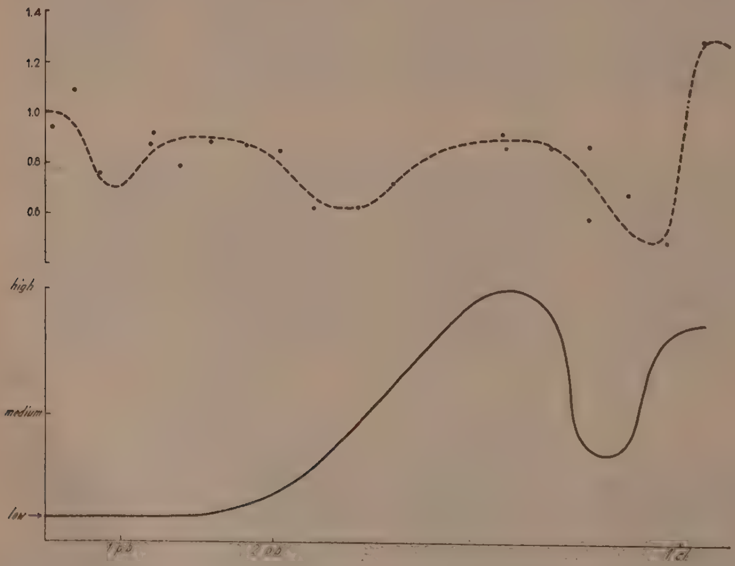

Fig. 8. Graph showing variations of tension at the surface (broken line) and of viscosity (full line) from oviposition till 1st cleavage. Abscissae: time. Ordinates: 1. tension at the surface, expressed in numerical value of $\frac{B}{L}$ (cf. text); 2. estimated relative value of viscosity.

at the surface" (HARVEY 1931). We may take for granted that there exists an inverse relation between this tension and the elongation produced. As a matter of fact, the elongation caused by the same force during the same length of time does not only depend upon the "tension at the surface", but upon other factors as well. The stretching forces appear only after the separation of the substances of different density at the poles of the egg has taken place; the time required for this separation grows with increasing viscosity of the egg. Likewise, with greater viscosity the rate of elongation will be slower. Therefore, when viscosity is high, the elongation of the eggs will be small; in comparing the results, it will be necessary to take the viscosity changes of the egg into account. After the centrifugal force is removed, the eggs gradually become spherical again. This recovery of the spherical form is, however, very slow; therefore, we may consider the shape of the egg precisely 5 minutes after the removal of the centrifugal force, as in the photographs of fig. 7, to be a measure of the distortion produced by centrifugation. This distortion can be expressed in the relation $\frac{L}{B}$ between the diameter L in the direction of the centrifugal force and the largest diameter B perpendicular to it. The inverse quotient $\frac{B}{L}$, therefore, will change in relation to the variations in "tension at the surface", provided that the viscosity of the egg does not change.

Applying these considerations to the experiment of fig. 7, it becomes clear that important changes of this tension take place during the uncleaved stage of the egg. In the eggs centrifuged shortly after laying, the quotient $\frac{B}{L}$ is about = 1.0 (0.94–1.09), indicating a relatively high "tension at the surface". 5 Minutes before the extrusion of the first polar body, a distinct drop has occurred, $\frac{B}{L} = 0.76$. In eggs centrifuged during the extrusion of the polar body, the elongation is still more pronounced. Between 1st and 2d maturation division, the tension is higher again, $\frac{B}{L}$ varying between 0.79 and 0.92 with an average of 0.87. A second drop occurs after the extrusion of the second polar body, $\frac{B}{L}$ being = 0.62 both at 16 and at 33 minutes after the 2d polar body. Then there is a gradual rise, $\frac{B}{L}$ attaining a value of 0.92 at 69 minutes before the first cleavage. As it corresponds in time to a rise in viscosity, no conclusion as to a change in the "tension at the surface" is allowed. Now the value $\frac{B}{L}$ drops again, attaining a minimum with 0.49 just before the 1st cleavage; the drop of the curve corresponds to a drop in viscosity; the minimum falls, however, at a time when viscosity is rising again. We may conclude, therefore, that the "tension at the surface" is low immediately before cleavage. In the last egg of fig. 7, centrifuged 10 minutes after cleavage, $\frac{B}{L} = 1.29$; probably, the tension is high again, but secondary factors, connected with the process of cleavage, may have come into play.

The results indicate, therefore, that the "tension at the surface" undergoes cyclic changes during the first hours of development of the *Limnaea* egg, being low 1. at first polar body formation, 2. some time after the extrusion of the second polar body and 3. immediately before cleavage, whereas it is higher before maturation and in the intervals between those minima (fig. 8).

5. Volume of formed components: In our recent paper (Raven & Bretschneider 1942), changes in the relative proportions of the zones in centrifuged eggs have been described. The experiment of fig. 7 enables us to evaluate these changes quantitatively. To this end, the volumes occupied by zone 1 (fat and vacuoles), 2 + 3 (hyaloplasm and α-granules) and 4 (β- and γ-granules), respectively, were calculated in the case of the eggs of fig. 7, Ns. 1, 2, 5, 9, 13, 17 and 18.

Fig. 9 shows the method of calculation. As the eggs are not spherical, the drawings taken from the photographs were treated in the following way: by the lines AB and CD the egg was divided into the parts I, II, III, IV and V (fig. 9 a). Part I, II, IV and V may be treated as spherical segments, and their volumes computed with sufficient accuracy. Part III, on the other hand, was treated as a slice of a sphere constructed inside the egg. By adding the volumes of I and II, and of IV and V, respectively, the volumes of the "fat" zone and of the "albumen" zone of the egg were obtained. The volume of III, diminished with those of II and IV, gives the volume of the zone of hyaloplasm and mitochondria. In other cases, as in the egg of fig. 7^{17}, the egg could be treated as a cylinder with two hemispheres at the ends, which made the calculation of volumes easier (fig. 9 b).

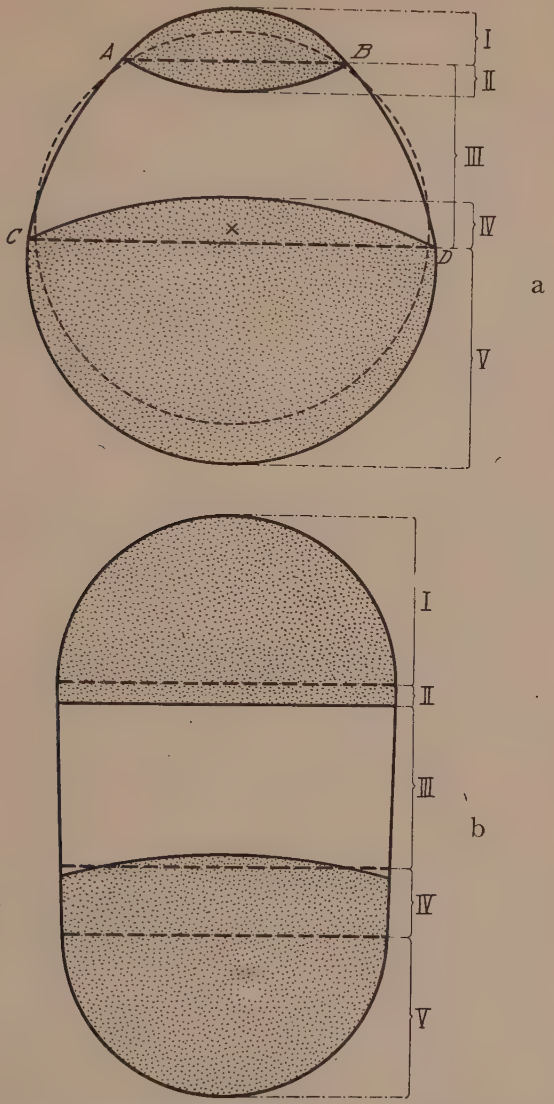

Fig. 9. Diagrammatic figures showing method of computation of egg substances. *a*. Egg 5 of fig. 7. Parts I, II, IV and V are treated as spherical segments; part III is equalized to a slice of an inscribed sphere (broken line). "Fat zone" = I + II, yolk zone = IV + V, hyaline zone = III–II–IV. *b*. Egg 17 of fig. 7. Parts I and V are treated as hemispheres, parts II, III and IV as cylinders.

Table II gives the results of these calculations:

TABLE II

Fig.	Stage	Zone 1		Zone (2 + 3)		Zone 4		Total volume in 1000 μ^3
		in 1000 μ^3	%	in 1000 μ^3	%	in 1000 μ^3	%	
7^1	27 min bef. 1st. p.b.	58	5.2	480	43.5	567	51.3	1105
7^2	18 min. bef. 1st p.b.	60	5.2	549	47.8	539	47.0	1148
7^5	12 min. aft. 1st p.b.	65	4.6	516	37.1	811	58.3	1392
7^9	3 min. aft. 2d p.b.	111	7.7	628	43.4	707	48.9	1446
7^{13}	68 min. bef. 1st cleav	345	25.7	472	35.4	522	39.0	1339
7^{17}	36 min. bef. 1st cleav.	424	29.5	500	34.9	511	35.6	1435
7^{18}	20 min. bef. 1st cleav.	567	38.8	460	31.5	435	29.7	1462

The total volume of the egg increases, in the time considered, from 1105.000 μ^3 to 1462.000 μ^3; the increase is not entirely regular. This is due, presumably, to the fact that the eggs come from 4 different egg-masses: 1; 2–9; 13 and 17–18 each belonging to one batch. Zone 1 increases from 5.2% to 38.8% of the total volume; zone 4 decreases from 51.3% to 29.7%; zone (2 + 3) shows a decrease from 43.5% to 31.5%. The absolute volume of this zone remains, however, relatively constant; with one exception, it varies between 460.000 μ^3 and 549.000 μ^3. The first rapid increase of the egg volume, during the first maturation (7^5), is brought about by a sudden rise of the absolute and relative volumes of the albumen zone, the other zones remaining nearly constant. At the next stage (7^9), the hyaloplasm and "fat" zone have increased, the albumen zone decreased in volume. Between 2d maturation and 1st cleavage, the hyaloplasm zone reverts to its former volume, the albumen zone drops below its original size. The increase of the egg volume comes, therefore, at the end entirely to the advantage of zone 1.

The results of our measurements give support to the explanation given in our former paper (Raven & Bretschneider l.c.): The water, absorbed by the egg, is attracted by the γ-granules lying in the albumen zone; this explains the initial increase in volume of this zone (7^5). At later stages, the vacuoles produced in this way are accumulated in the lighter egg regions; this brings about a temporary increase in size of the zone of hyaloplasm (7^9), together with a decrease of the albumen zone. Finally, all these vacuoles gather in the "fat" zone; the hyaloplasm regains its former size, the albumen zone has diminished in consequence of the loss of γ-granules. It follows from Table II that the augmentation of zone 1 with $\pm 500.000 \mu^3$ results from a decrease of the albumen zone of $\pm 130.000 \mu^3$ and an increase of total egg volume of $\pm 360.000 \mu^3$. It might be conjectured, then, that the γ-granules absorb, on an average, about 3 times their own volume of water.

Clement (1938) calculated the volumes of the different zones in the centrifuged egg of *Physa heterostropha* from measurements of the spheres of different materials which pulled off during centrifuging. Comparison of his Table 1 with our Table II shows a full agreement as to the relative proportions of the layers. As in *Limnaea*, in the eggs of *Physa* between the time of laying and first cleavage the volume of the "fat" zone increases tenfold, that of the albumen zone decreases a little (15–25%), while that of the clear zone shows no change. In view of the difference of species and the different methods of centrifugation and computation the agreement is rather astonishing.

Costello (1939) calculated the relative volumes occupied by the formed components of centrifuged marine eggs. The results show that the relative proportions of the zones vary widely in different species. The fat zone varies between 1 and 25%, the yolk zone from 20–77%, the hyaline zone from 18–60%.

VITAL STAINING

Observations of Spek (1930–1934) on the eggs of diverse invertebrate animals and of Teleosts with the aid of vital dyes and indicators have shown that in these eggs, prior to or immediately after the beginning of cleavage, a "bipolar differentiation" occurs, leading to an accumulation of alkaline substances in the animal and of acid materials in the vegetative part of the egg. They were confirmed and extended by Ries & Gersch (1936) and by Raven (1938). It was shown that not only the pH, but also the rH of the egg protoplasm became different at opposite poles of the egg. It is especially the accumulation of the acid albuminous yolk in the vegetative hemisphere which is responsible for these differences.

Eggs of *Limnaea*, at various moments during the uncleaved stage, were stained with the following vital dyes: neutral red, nile blue chlorhydrate, brilliant cresyl violet, "Cresylechtviolet", methylene blue and its leucobase (rongalite white), Janus green, trypan blue. Partly, they were transferred to the diluted dye solutions while enclosed in their capsules; in other cases, they were delivered from their capsules prior to staining.

Neutral red: eggs stain rather intensely orange-red; the area of clear protoplasm at the animal pole remains colorless, the polar bodies are not stained. When the eggs are left in the dye, a ring of red granules appears around the animal pole at the margin of the clear area.

Nile blue chlorhydrate: eggs greenish blue with colorless polar area. Polar bodies colorless, in the 1st polar body brownish granules may be seen. Sometimes, however, the 1st polar body stains intensely blue. The cause of this difference in staining reaction is not clear; perhaps, in the last-mentioned case the polar body is dead.

Brilliant cresyl violet: the eggs are orange-brown with red violet tinge; this is at the animal side more distinct, whereas in the vegetative half the orange-brown color prevails. The polar area is colorless; the 1st polar body is red violet; later, violet granules appear; the 2nd polar body is colorless or orange-red.

With "Cresylechtviolet" the results are similar.

Methylene blue: in a weak solution of methylene blue, the intact eggs remain colorless or nearly so; only the polar bodies stain intensely blue. Cytolysed eggs, however, take the stain immediately and become greenish blue.

When the eggs are treated with the leucobase ("rongalite white"), the results are different. Within a minute, the eggs become deep blue all over; no color differences between the poles of the egg could be observed. It seems, therefore, that whereas methylene blue can enter only into damaged eggs, its leucobase penetrates into the eggs more easily; this may be due, however, to an injurious effect of the rongalite on the eggs, rendering the egg cortex more permeable to the dye. It has been observed, by treating cleaving eggs with rongalite white, that only in weakly colored eggs the cleavage was continued; in those eggs which stained intensely, it stopped nearly immediately.

Janus green: The intact eggs stain very weakly; only after some time they take a light green tinge. The polar bodies become dark green. Cytolysed eggs are stained immediately. In a few instances, the eggs were kept in a weak solution of Janus green under a sealed cover slip; no change of the color to red, indicating a reduction of the dye to diethylsafranin, has been observed.

Trypan blue: the eggs remain colorless or nearly so. Only the polar bodies take the stain and become deep blue.

The results of the vital staining experiments may be summarized in this way: with neutral red, nile blue chlorhydrate, brilliant cresyl violet and "Cresylechtviolet" the eggs stain rather intensely; methylene blue penetrated only in its reduced form; whereas Janus green and trypan blue did hardly stain the intact eggs at all. Cytolysed eggs, however, stained intensely in a few moments. The clear polar area of maturing eggs remains colorless in all instances; the dye is bound, therefore, to the yolk; in the case of neutral red, an accumulation in granular form has been observed. The polar bodies behave differently; they may remain colorless or take the stain intensely.

No differences in color, ascribable to differences in pH or rH in different regions of the egg, have been observed. Only in brilliant cresyl violet and "Cresylechtviolet", the animal and vegetative halves show a somewhat different hue; as, however, the vegetative side is orange-brown in color, which does not belong to the normal color range of these dyes, the interpretation of this fact is difficult. Probably, this color is a mixture of the own yellow pigment color of the yolk and a reddish tinge produced by the dye.

We must conclude, therefore, that, apart from the withdrawal of the yolk granules from the animal pole of the egg during maturation, in the eggs of *Limnaea stagnalis* no "bipolar differentiation" in the sense of Spek has been observed.

HISTOCHEMICAL REACTIONS

1. Fat: In eggs fixed in formalin, then treated with Sudan III or scharlach, small bright red fat droplets may be seen scattered through the protoplasm. During maturation, they leave free the clear area with the maturation spindle at the animal pole.

After treatment with osmic acid, the distribution of the fat droplets may be studied in sectioned eggs. Their dispersion is not altogether regular, groups of larger droplets alternating with smaller ones in a rather irregular manner. No or only a few fat droplets are found in the maturation spindle and asters and in the egg cortex; they are absent also in the pronuclei. Their density is in the ectoplasm of the vegetative hemisphere somewhat greater than in the rest of the egg; on the contrary, the animal pole plasm contains a smaller number of fat droplets. They lie in the meshes between the vacuoles.

2. Glycogen: In an egg, fixed in alcohol some time after the completion of the second maturation division and stained with Best's carmine, a halo of bright red granules was surrounding the remnant of the maturation aster, and finer red granules occupied the whole aster area. Larger granules were found

sporadically in the egg cortex. In control preparations, treated with saliva prior to staining, these granules do not appear. This proves the stained matter to be glycogen. Its localization, together with the fact that in centrifuged eggs the glycogen is found in the 3d zone (RAVEN & BRETSCHNEIDER l.c.), suggests a relationship existing between the glycogen and the α-granules of the egg.

3. Thymonucleic acid: The distribution of thymonucleic acid was studied with the Feulgen reaction. The egg chromosomes in the maturation spindle and in the polar bodies are intensely stained. When maturation is completed and the karyomeres of the egg nucleus are formed, the coloration diminishes in intensity. The sperm-head in its subcortical position is an intensely stained red body. Later, the pronuclei contain scattered red granules.

The cytoplasm, in Feulgen-stained eggs, takes the stain, too. In centrifuged eggs, especially the β-granules of the 4th zone are distinctly red; the coloration of the hyaloplasm is weaker, the maturation spindle being somewhat darker than the surrounding plasm. As, however, these structures are stained also in control preparations treated with Schiff's reagens without preceding hydrolysis, this coloration of the cytoplasm and yolk is not due to thymonucleic acid.

4. Pentosenucleic acids: BRACHET has recently (1942) published a histochemical reaction for the detection of pentosenucleic acids. It is based on 1. the strong affinity of pentosenucleoproteids for pyronine, when stained with methyl green-pyronine after UNNA-PAPPENHEIM, 2. the specific action of the enzyme "ribonuclease" upon pentosenucleic acids. With the aid of this method, the distribution of pentosenucleic acids in the egg was studied. After staining with methyl green-pyronine, the β-granules show a deep brick red coloration; the γ-granules have a pink color, the hyaloplasm is light violet red. Especially in centrifuged eggs these color differences are very striking. In sections, treated with ribonuclease before staining with methyl green-pyronine, the β-granules and the hyaloplasm are colorless, the γ-granules, on the contrary, show the same pink color; control preparations, treated with distilled water only, show no diminution of the color as compared with untreated sections. Slides, treated with ribonuclease, and stained afterwards with iron haematoxylin and eosin, show no peculiarities; all the

normal components of the egg are present. It may be concluded from these observations that the cytoplasm of the *Limnaea* egg contains pentosenucleic acids, which are especially accumulated in the β-granules; they are rather insoluble in water, but are broken down by the action of ribonuclease.

5. Glutathion: The reaction with alkaline sodium nitroprussiate was positive both when it was done in the manner described by Ries (1937) and after Lison (1936, p. 136). The latter method has the advantage of permitting a discrimination between glutathion in its reduced and oxydized form and sulfhydril components bound to proteids. When the reaction was done immediately after the eggs were delivered from their capsules (using a 10% solution of sodium nitroprussiate), a distinct pink color appeared flash-like in an annular zone surrounding the area of the nucleus or maturation spindle. A preliminary treatment of the egg with KCN did not increase the strength of the reaction. After a prolonged treatment with trichloracetic acid, however, an intense deep red coloration of the whole egg, being strongest in its central part, was observed. We may conclude, therefore, that the egg of *Limnaea* contains both free glutathion, in its reduced form, being concentrated in the neighbourhood of the maturation spindle, and sulfhydril components bound to proteids, which are dispersed in the egg protoplasm, but especially in its central part.

6. Phenolases: With the M-nadioxydasereaction small granules of indophenol blue are formed; they are distributed rather evenly on the egg surface, but leave free the area of clear protoplasm at the animal pole of the maturing egg and the polar bodies.

7. Peroxydases: The reaction with benzidine and H_2O_2 is clearly positive. Small blue granules are formed in the egg, distributed regularly on the surface; their density is somewhat less than that of the indophenol blue granules in the preceding experiment.

As in centrifuged eggs both the phenolase and the peroxydase-reaction are almost entirely restricted to the zone of α-granules, the enzymes seem to be bound to these granules. It is possible, however, that this localization of the reaction is due to a secondary absorption of the stained reaction products at the granules (cf. Lison 1936).

SUMMARY

The structure and physico-chemical composition of the egg of *Limnaea stagnalis* and the changes occurring during the uncleaved stage of the egg were studied by a variety of methods.

A. Composition of egg:

1. The cytoplasm of the egg consists of 2 parts: ectoplasm and endoplasm, which differ in their staining reactions. Immediately after oviposition, the ectoplasm occupies a sector at the vegetative pole of the egg, the endoplasm the rest of the egg.

2. Three sorts of granules can be distinguished: α-granules (probably mitochondria), β-granules and γ-granules. Moreover, fat droplets and Golgi bodies are present in the egg.

3. The α-granules, which are small, are accumulated especially in the endoplasm. Probably, glycogen, phenolases and peroxydases are bound in some way or other to these granules.

4. The β-granules, of medium size, form a major part of the ectoplasm. They consist of albumen and contain pentosenucleic acids.

5. The γ-granules are coarse, probably albuminous in nature; they lie mostly in the endoplasm.

6. Both fat droplets and Golgi bodies are distributed rather evenly in the cytoplasm, leaving free only the spindle and asters. "Praesubstances" and "Golgi systems" can be distinguished.

7. The hyaloplasm contains pentosenucleic acids in small quantity and, probably, bound sulfhydril components, especially in its central part.

8. The freshly laid egg contains the first maturation spindle in metaphase. The spindle area is free of fat droplets and Golgi bodies, but is characterized by the presence of free glutathion in reduced form. The chromosomes contain thymonucleic acid.

B. Changes during uncleaved stage:

9. The course of the maturation divisions and the formation of the polar bodies are described. The egg shows amoeboid movements shortly after the extrusion of either of the polar bodies. This is accompanied with a distinct drop of the tension at the surface.

10. The α- and γ-granules of the endoplasm are attracted by the maturation spindle and asters, forming a halo surrounding the amphiaster.

11. The ectoplasm spreads beneath the egg cortex to the

animal side. At first, a gap remains at the animal pole; after the completion of the maturation divisions, the ectoplasm surrounds the whole egg.

12. A fine chorion is formed, which lies inside the first, but outside the second polar body.

13. The spermaster makes its appearance shortly before the extrusion of the first polar body; during the maturation divisions, it grows slowly. This is accompanied with a gradual rise of the viscosity of the protoplasm. No division of the spermaster with formation of an amphiaster takes place.

14. The sperm-head remains in a subcortical position till shortly after the extrusion of the second polar body; then, it migrates to the spermaster and develops into the male pronucleus.

15. The chromosomes left in the egg after the maturation divisions swell into karyomeres which fuse to the female pronucleus.

16. The copulation of the pronuclei takes place immediately beneath the egg cortex at the animal pole.

17. About one hour before cleavage, the animal pole plasm is formed by a local accumulation of substances attracted, probably, by the egg cortex at the animal pole. The centripetal flow of protoplasm in the dilating maturation aster may aid in this localisation process. Many α-granules are transported by it to the animal pole plasm.

18. From the time of oviposition till first cleavage the egg swells considerably, probably by the intake of water. This is accompanied with a decrease in density. At the same time, the γ-granules of the egg give rise to the formation of vacuoles, by an attraction of water from the neighbourhood. Eventually, the egg protoplasm has a vacuolated appearance throughout, with the exception of the animal pole plasm.

19. The viscosity, which is high one hour before cleavage, has a minimum 30 minutes later, then it rises again. The tension at the surface reaches a minimum immediately before the beginning of cleavage.

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EINIGE NEUE THEORIEN ÜBER DIE MUSKELBEWEGUNG

NACH EINEM VORTRAGE, GEHALTEN IN DER VERSAMMLUNG DER NEDERLANDSCHE DIERKUNDIGE VEREENIGING ZU UTRECHT AM 13. MÄRZ 1943

VON

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Es ist nicht die Absicht des Verfassers die Ergebnisse eigener Versuche mitzuteilen, seine Aufgabe ist, zusammenfassend die Lehre einiger bekannter Forscher zu referieren.

Es ist kaum ein energieliefernder Prozess denkbar, den man nicht zur Erklärung der Muskelverkürzung herangezogen hätte. Wir nennen: Oberflächenspannung, Quellung, Osmose. Vor allen Dingen hat die Quellungstheorie die Wissenschaft eine Zeitlang beherrscht, seitdem unser Wissen über die Bildung von Milchsäure beim arbeitenden Muskel einigermassen vertieft worden war. Man glaubte fest an die Möglichkeit anisodiametrischer Verkürzung durch Quellung, da ja Taue, wenn sie nass werden, sich zusammenziehen. Man vergass, dass die Fasern der Taue spiralförmig um einander gewunden sind, Muskelfasern nicht; ausserdem zeigten Berechnungen, dass man durch Milchsäure die 50% Verkürzung, deren die Muskelfaser fähig ist, niemals würde erklären können. Ähnliches Schicksal hatten die anderen Theorien, sobald man sie strenger Kritik unterwarf. (Man lese diesbezüglich O. MEYERHOFS Kritik in Bethes Handbuch der Physiologie, 8, 1, p. 530.)

Vollkommen neue Gesichtspunkte lieferten Forschungen aus der Schule J. BARCROFTS, durch welche sich ergab, dass ein Teil der erzeugten Wärme sowie der Sauerstoffverbrauch erst *nach* der Muskelverkürzung nachgewiesen werden kann. Auch die Milchsäure tritt erst nach der Verkürzung auf, ist also nicht die Ursache der Kontraktion, sondern ihr Entstehen wird durch die Kontraktion verursacht. Dies wurde vor allem durch E. LUNDSGAARD (1930, 1931) bewiesen. Er hemmte die Fähigkeit des Muskels Milchsäure zu bilden durch Monojodessigsäure, ohne die Kontraktilität aufzuheben.

F. VERZÁR (1912) hat den Sauerstoffverbrauch des ruhenden und des tetanisierten Musculus gastrocnemius der Katze in seiner zeitlichen Abhängigkeit vom Tätigkeitszustande gemessen.

TABELLE 1

Versuch 1.	Ruheverbrauch pro g/min	0,00670	cm^3 Sauerstoff
	Tetanus:		
	Verbrauch während Tetanisierung p.g/min	0,00196	,, ,,
	61 sec später p.g/min	0,01580	,, ,,
	73 sec später p.g/min	0,00960	,, ,,
	Nach Pause von über 3 Minuten erneuter Tetanus:		
	Verbrauch während Tetanisierung p.g/min	0,00397	,, ,,
	80 sec später p.g/min	0,01360	,, ,,
Versuch 2.	Ruheverbrauch pro g/min	0,00303	cm^3 Sauerstoff
	Tetanus:		
	Verbrauch während Tetanisierung p.g/min	0,01080	,, ,,
	15 sec später p.g/min	0,02030	,, ,,
	11 sec später p.g/min	0.01260	,, ,,
	11 sec später p.g/min	0,00935	,, ,,
	146 sec später p.g/min	0,00358	,, ,,

Sauerstoffverbrauch des M. gastrocnemius der Katze. Gemessen wird 1) der Sauerstoffverbrauch pro g/min in der Ruhe; 2) idem während der Tetanisierung; 3) der Sauerstoffverbrauch pro g/sec in verschiedenen Zeitabständen je zwischen zwei Messungen. Aus Versuch 2 ergibt sich, dass der sehr geringe Sauerstoffverbrauch während beider Tetanisierungen bei Versuch 1 keiner festen Regel entspricht. (Nach Verzár).

Als Folge des gegebenen faradischen Reizes, der 25 sec dauerte, verbrauchte der Muskel mindestens 220 sec lang mehr Sauerstoff als in der Ruhe. Während er in der Ruhe in dieser Zeit 0.260 cm^3 Sauerstoff verbraucht haben würde, verbraucht er nunmehr 0.753 cm^3 Sauerstoff. Die Reizung ist daher verantwortlich für mindestens 0.5 cm^3 Sauerstoff, die der Muskel verbraucht hat. Durch andere Versuche weiss man seither, dass es zur Kontraktion überhaupt keines Sauerstoffs bedarf.

Diese Ergebnisse passen gut zu den Resultaten von A. V. Hill (1913), der die Wärmeabgabe des gereizten Muskels gemessen hat. Wenn der Muskel sich in reinem Stickstoff befindet, so erzeugt er bei der Kontraktion unmittelbar nach der Reizung Wärme, danach aber nicht mehr. Steht dem Muskel aber Sauerstoff zur Verfügung, so erzeugt er noch lange nach Reizung und Kontraktion weiterhin Wärme (J. Barcroft (1914), Fig. 41, pag. 78). Innerhalb 4–5 Minuten nach Reizung durch Einzelschlag wird ebensoviel Wärme abgegeben, als in der kurzen Zeit direkt nach der Reizung. Die später auftretende Wärme entspricht der bei Anwesenheit von Sauerstoff auftretenden Oxydation der Milchsäure (FLETCHER und HOPKINS, 1907). Der Sauerstoffverbrauch bei Wiederherstellung und die Wärmeerzeugung sind daher zu vergleichen mit dem, was bei der Arbeit etwa einer Dampfmaschine geschieht, die Akkumulatoren lädt und daher potentielle Energie erzeugt, bereit, um unmittelbar in kinetische Energie umgesetzt zu werden, nämlich in unserm biologischen Fall in Muskelverkürzung oder richtiger Muskelspannung.

Seitdem die Resultate dieser Versuche allgemein bekannt wurden, hat die Untersuchung des Chemismus der Muskelverkürzung grosse Fortschritte gemacht. Diese Untersuchungen wurden zunächst noch in der Hoffnung unternommen, durch die gefundenen chemischen Reaktionen die Verkürzung selbst erklären zu können. Zumal die Kenntnis energieliefernder anaerober Prozesse nahm stark zu. Neben Glykogen spielen beim Muskelchemismus noch die folgenden Stoffe eine Hauptrolle: Adenyltriphosphorsäure, Creatinphosphorsäure („Phosphagen"), die beide, sich spaltend, Phosphorsäure liefern, die mit dem eigentlichen Treibstoff, dem Kohlehydrat die Hexosemonophosphorsäure („Lactacidogen") bildet. Die Bedeutung dieser Phosphorylierung ist zwar unbekannt, viele aber sahen in der Phosphorylierung ein Mittel, die Spaltungsprozesse des Glycogens, durch welche sich Milchsäure bildet, zu beschleunigen. A. V. HILLS (und Mitarbeiter, vor allem W. HARTREE 1928, 1930) feine Wärmemessungen erlaubten diesem Forscher, die Prozesse beim Muskel und beim Nerven in einzelne Phasen zu zerlegen: 1) Initiale Wärmebildung, 2) Verzögerte Wärmebildung. Die initiale Wärmebildung verläuft anaerob und findet noch während der Kontraktion statt. Die verzögerte Wärmebildung verläuft zu einem sehr kleinen Teil anaerob, zum grössten Teil, ebenso viel oder mehr als die initiale Wärme, aerob. Diese Fraktion kommt daher nach der Verkürzung, d.h. während der Erschlaffung, als sogenannte Wiederherstellungswärme (Erholungswärme), da ja nach jeder Verkürzung der Zustand der Verkürzungsbereitschaft wiederhergestellt werden muss. Heute betrachtet man den gesamten Chemismus, soweit er bekannt ist, als zum Wiederherstellungsprozess gehörig, während man über die Energiequelle der Verkürzung nichts mit Gewissheit weiss. Daher ist jegliche Theorie, die in dem bekannten Chemismus direkt oder indirekt die Ursache, also eine Erklärung der Verkürzung sieht, falsch. Wir werden hierauf, bei Gelegenheit der Besprechung der spannungslosen Verkürzung zurückzukommen haben. Auf den folgenden Seiten ist es unsre Aufgabe einige neuere Versuche und Theorien, welche die Ursache der Verkürzung betreffen, vorzutragen.

I. Die neueren Ergebnisse der Untersuchungen über die Muskulatur, durch die Technik des Versuches an isolierten Muskelfasern von J. LINDHARD und seinen Mitarbeitern (1939)

Die Elektrophysiologie der isolierten Muskelfaser

Ältere Auffassang über den Aktionsstrom des Muskels

Man betrachtete den Aktionsstrom des Muskels sozusagen als Fortsetzung des Nervenstroms. Man meinte, dass sich vom Eintritt des Nerven in die Muskelfasern eine Kontraktionswelle über den gesamten Muskel fortpflanzt, die von der elektrischen Erscheinung des Aktionsstromes begleitet wird. Daher sei der Aktionsstrom, gleich dem Aktionsstrome des Nerven, diphasisch d.h. der Muskelstrom sollte auf einer Fortbewegung von Negativität beruhen (siehe fig. 1 und die Erklärung davon). Nach

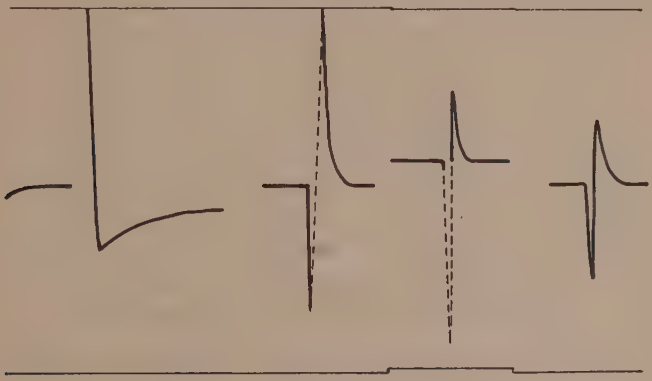


Fig. 1. Aktionsströme von einzelnen Muskelfasern der Eidechse. Direkte mechanische Reizung der Endplatte, Ableitung von der Faser und durch eine zweite Elektrode, die am Rande der Endplatte lag (nach ASMUSSEN und LINDHARD). In einigen Fällen ist die Kurve zwar diphasisch aber beide Phasen sind nicht symmetrisch (vor allem links). Die erste Phase entspricht offenbar einem andern Prozess als die zweite (Siehe Text).

S. Tschirjew (1913), gibt es solch eine Welle von Negativität im Muskel nicht. Man erhält diphasische Aktionsströme auch dann, wenn man die Ableitungselektroden so auf den Muskel aufsetzt, dass die Ableitung nicht longitudinal, also in der praesumptiven Richtung der Fortbewegung, sondern transversal erfolgt (siehe auch V. Henriques und J. Lindhard (1920)).

Der Reizstrom in der Endplatte

Der mit der früheren Technik gemessene Aktionsstrom ist überhaupt nicht eine Äusserung der Muskelfaseraktivität, sondern er wird durch die Endplatte erzeugt. Der Strom der der Faserkontraktion entspricht, ist bei Totalableitung zu schwach um sich isoliert geltend zu machen. Der Strom, den die kleine Endplatte erzeugt, bleibt auf seinen Ursprungsort beschränkt. Von einer elektrischen Welle, die der Kontraktionswelle folgte, ist daher keine Rede.

Der Endplattenstrom ist ein Analogon der oft sehr starken elektrischen Schläge, die zu erteilen verschiedene Fischarten imstande sind. Bei den meisten elektrischen Fischen sind die elektrischen Organe phylogenetisch und ontogenetisch von der Muskulatur abzuleiten; die Fasern spielen dabei keine Rolle, sondern die Platten der elektrischen Organe entsprechen lediglich den Endplatten der Muskeln. Doch liefern auch diese Organe Ströme, die in Gestalt einer Optimumkurve registriert werden. Steigen, Optimum und Sinken der Kurve entspricht der Zahl der Platten die an der Stromerzeugung successiv teilnehmen: erst wenig, bis zum Optimum in zunehmender Anzahl, dann abnehmend, sodass die Optimumkurve auch hier keineswegs der Ausdruck sich fortbewegender Negativität ist. Auf diesen Ergebnissen baut die Lehre von Buchthal und Lindhard sich auf, dass es in der Muskelfaser jeweils einen lokalen Endplattenstrom, daneben aber auch einen Faserstrom gibt, Ströme, die wir als Reiz- und Kontraktionsstrom kennen lernen werden.

Die beiden Arten der elektrischen Ableitung (fig. 2)

a) Beide unpolarisierbaren Ableitungselektroden kommen im Mikroapparat auf zwei Punkte der gleichen Faser eines Muskels von *Lacerta* (F—F Ableitung). b) Eine Elektrode kommt auf die Endplatte, die andere auf die entsprechende Faser (F—E Ableitung).

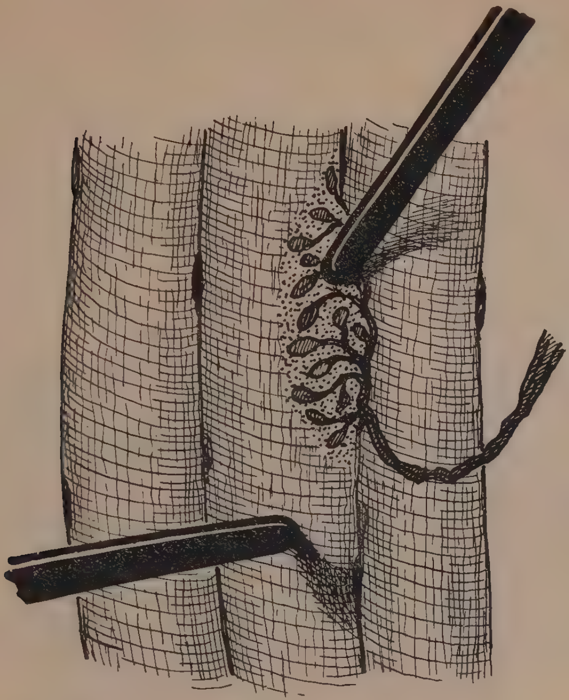


Fig. 2. Muskelbündel von einer Eidechse, ein Bündel lebender, nicht gefärbter Muskelfasern. Obere unpolarisierbare Ableitungselektrode auf der Endplatte, untere Elektrode auf gleicher Faser (F—E Ableitung). Vergrösserung 450 mal. (Nach BUCHTHAL und LINDHARD)

Die F—E Schwankung wird dadurch hervorgerufen, dass die Endplatte tetanisch gereizt wird; die Faser dient hierbei lediglich zur Ableitung. Scheinbar ist in manchen Fällen die registrierte Potentialschwankung einem diphasischen Aktionsstrome gleich. Allein beide Phasen sind nicht symmetrisch, da sie in der Tat aus zwei aufeinanderfolgenden Schwankungen bestehen: dem Reizpotential und dem Verkürzungspotential, die beide an und für sich monophasisch sind. Die Ausschlagsrichtung des Kathodenstrahlen-oscillogramms kann zwei einander entgegengesetzten, oder, in andern Fällen, einander gleichgerichteten Schwankungen entsprechen.

Bei direkter Reizung der Faser tritt keine Schwankung des F–E Potentials auf

Wenn man das F—F Potential mit zwei unpolarisierbaren

Elektroden misst, die man jeweils mit verschiedenem Abstand von einander auf die Muskelfaser setzt, so nimmt das F—F Potential mit dem Abstand zwischen beiden Elektroden zu. Offenbar ist daher das Potential der Länge der zwischen den Elektroden liegenden Muskelfaserstrecke proportional. Bei dem F—E Potential war eine entsprechende Grössenänderung nicht nachweisbar. Immer aber ist das F—E Potential viel grösser als das F—F Potential (fig. 3). Bei einem bestimmten Elektrodenabstand war das F—F Potential 0.5 à 1.0 mV. Bei gleichem Elektrodenabstand war das F—E Potential 10 mV. Das Verhältnis ist also ungefähr 1 : 10. Hierdurch wird die Tatsache verständlich, dass bei elektrischen Fischen

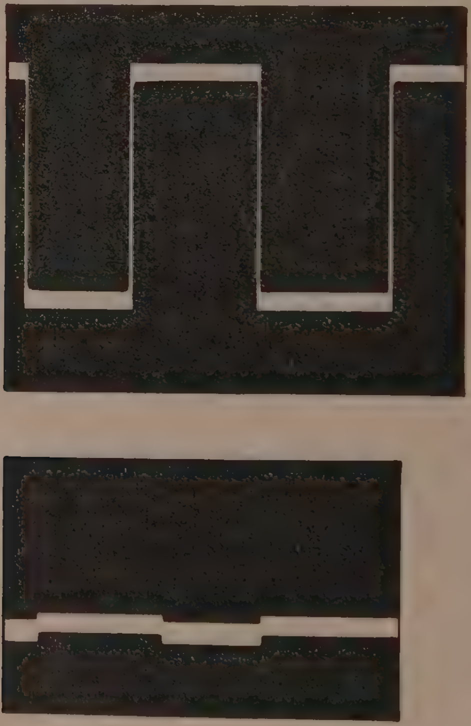


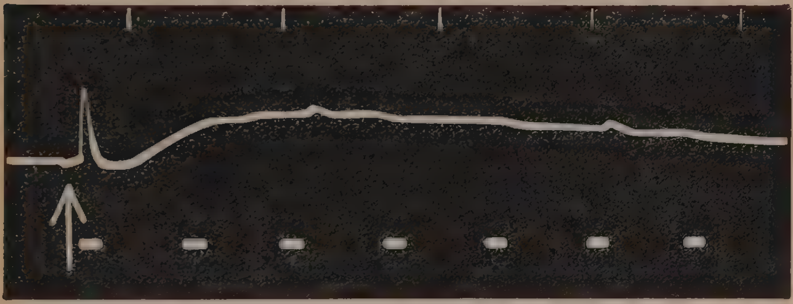
Fig. 3. Potentialsprung zwischen motorischer Endplatte und Faser (F—E Ableitung, oberste Kurve) und zwischen zwei Punkten auf der gleichen Faser (F—F Ableitung, untere Kurve). Abstand zwischen beiden Elektroden ist in beiden Fällen der gleiche. (Nach Buchthal und Lindhard)

das grosse Endplattenpotential zu Angriffs- oder Verteidigungszwecken verwendet wird.

Ruhepotential und Aktionspotential

Das Ruhepotential besteht dauernd, bis der Muskel gereizt wird. Bei direkter Reizung der Muskelfaser nimmt das Ruhepotential und nur dieses ab. Hierauf folgt die Wiederherstellungsperiode, in welcher sich das Ruhepotential vollkommen wieder herstellt. Man misst das Reizungspotential (wie üblich) am

a.



b.

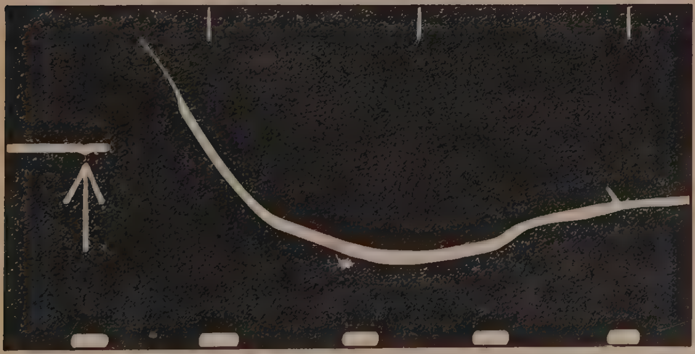


Fig. 4a. Potentialsprung, bei Reizung und Verkürzung einer indirekt gereizten Froschmuskelfaser. Das Potential der ruhenden Faser (4 mV) ist kompensiert. Der Pfeil entspricht dem Augenblick der Reizung. Entfernung zwischen je zwei Zeitmarken 20 msec. Reizungs- und Verkürzungspotential schwanken in gleicher Richtung

Fig. 4b. Alles wie in fig. 4a, nur verlaufen beide Schwankungen in entgegengesetzter Richtung

besten nach Kompensation des Ruhepotentials, daher als Ausschlag des Oscillographen.

Wenn man die Endplatte reizt, dadurch, dass man eine der beiden Reizelektroden in die Nähe des Nervenendes legt, nimmt man zweierlei Veränderungen des Ruhepotentials wahr: a. 1 bis 2 msec nach dem Reiz tritt eine Verminderung des F–E Potentials um ungefähr 1/10 des Ruhewertes auf, die sich 2 bis 3 msec lang behauptet. b. Hierauf erst folgt die Veränderung des F–F Potentials. Die Aktionsströme, die auf diese Weise aufeinander folgen, sind also beide Verminderungen der Ruhepotentiale. Sie können gleichgerichtet sein oder, verglichen mit einander, in entgegengesetzter Richtung verlaufen (fig. 4a und b).

Bestätigung dieser Resultate durch Ausschaltung der Endplatte durch Curarin (Tabelle 2)

Sobald die Endplatte vollkommen funktionslos geworden ist, treten nicht mehr zweierlei Ströme von in vielen Fällen entgegengesetzter Richtung auf. (Siehe die Erklärung von Tabelle 2).

TABELLE 2

Normal			Curarin		
F–E	F–F	Häufigkeit	F–E	F–F	Häufigkeit
+ 70	+ 6	4 ×	+ 6	+ 5	7 ×
+ 33	− 3	4 ×	+	−	0 ×
− 74	+ 8	3 ×	−	+	0 ×
− 65	− 5	5 ×	− 6	− 7	6 ×

Tabelle 2, verkürzt nach Tab. VII von Buchthal und Lindhard, 1939, p. 91. Die dritte Kolumne, sowohl unter *Normal* als unter *Curarin*, gibt die *Häufigkeit* wieder, mit welcher auf der ausführlichen Tabelle: gleiche Stromrichtung van F–E und F–F, oder ungleiche Richtung, F–E positiv, oder F–F positiv vorkommt. Man beachte, dass, solange die Endplatte funktioniert (Normal), jede dieser Möglichkeiten ungefähr gleich oft realisiert ist. Nach Ausschaltung der Endplatte durch Curarin sind die Ströme bei beiden Ableitungen immer gleichgerichtet und ungefähr gleich stark, während sie bei der normalen Faser, was die Stromstärke betrifft, sich ungefähr wie 10 : 1 verhalten. Die Stromstärke ist jeweils in Massen für die Ausschläge des Oscillographen angegeben.

Die Endplatte ist dann nichts anders mehr als ein Ableitungsort geworden. Sie liefert keinen eigenen Strom mehr. Es bleibt nur das F–F Potential oder der F–F Aktionsstrom übrig. In diesem Zustande ist die Muskelfaser nicht mehr indirekt reizbar, nur noch direkt. Dadurch zeigt sich also, dass das F–E Potential einer Erscheinung entspricht, durch welche die Erregung vom Nerven auf den Muskel übertragen wird. Man kann die Endplatte auch durch Radiumemanation lähmen; allein dieses Mittel wirkt nicht spezifisch auf die Endplatte wie Curarin, sondern vernichtet auch die Faserwirkung, sodass die Faser dann auch nicht mehr direkt reizbar ist. In diesem Zustande kann weder das F–E, noch das F–F Potential gemessen werden.

Die Muskelfaser und das Alles- oder Nichts-Gesetz

Der Wert des Alles- oder Nichts-Gesetzes für unsre Einsicht in das Wesen der Nervenleitung, beruhte auf der Feststellung, dass der Nerv nicht irgendwelche Energie leitet, die ihm aus einem Zentrum in geringerem oder grösserem Ausmass zugeführt wird.

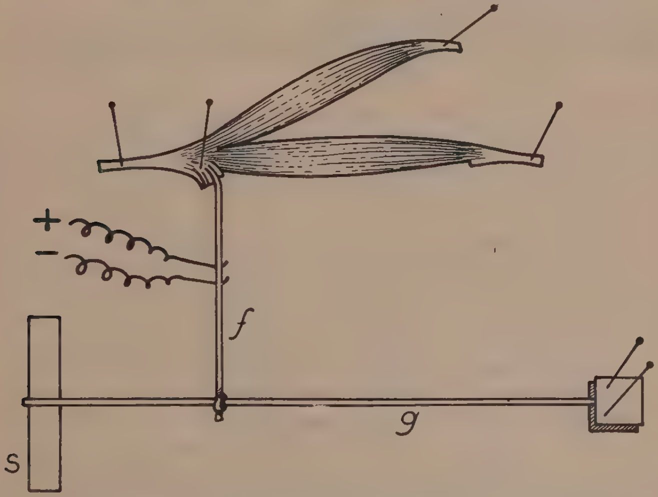


Fig. 5. Versuchsanordnung zur Registrierung der Spannung einer einzelnen Faser aus dem M. semitendinosus vom Frosch: *f* ist die isolierte Faser des durch Stecknadeln fixierten Muskels; sie kann vom Nerven des Muskels aus indirekt, von dem gezeichneten Elektrodenpaar aber direkt gereizt werden; *g* ein Glasstäbchen, das rechts befestigt ist, links auf einer Skala *s* frei beweglich ist und die Spannungsveränderungen der Faser isometrisch abzulesen erlaubt. (Nach Asmussen)

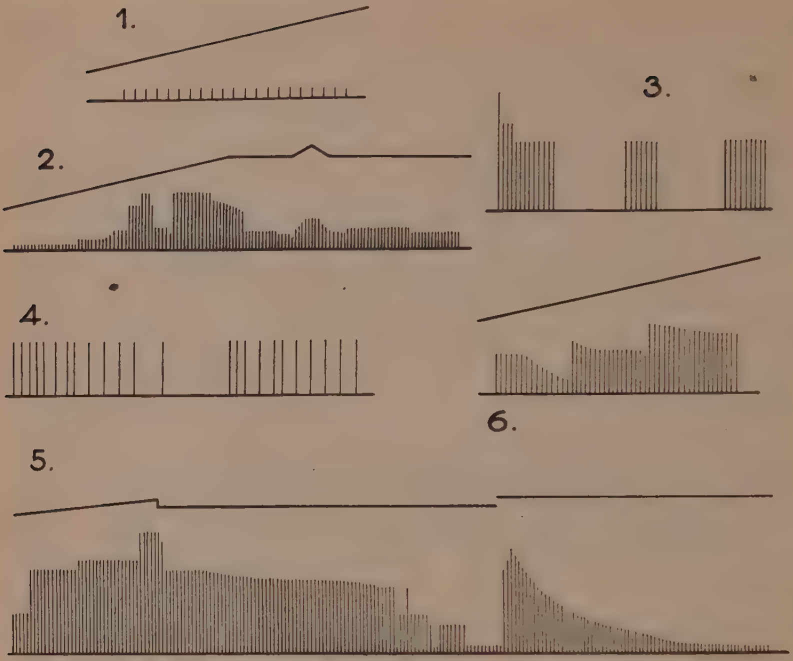


Fig. 6. Alles- und Nichtsgesetz des Muskels der Eidechse. Einzelne Faser (Präparat siehe fig. 5), oder Bündel von einigen Fasern. Spannung nach Massgabe der Reizstärke, Spannungsunterschiede nach Massgabe der Anzahl Fasern, für die der Reiz überschwellig ist, oder der Ermüdung. 1. Einzelne Faser; indirekte Reizung. Die oberste Kurve gibt die Reizstärke an. Das Alles- oder Nichtsgesetz gilt (Konstanz der jeweils erzeugten Spannung); sein Sitz ist jedoch die motorische Endplatte (indirekte Reizung). 2. Bündel von 8 Muskelfasern, indirekte Reizung. Reizstärke: oberste Kurve. Erst je nach Reizstärke, später je nach Ermüdung tritt die Spannung in deutlichen Abstufungen auf, die jedoch durch Gereiztwerden oder Ermüdung von mehr oder von weniger Fasern bedingt werden. 3. Kleines Bündel von Muskelfasern, indirekte Reizung von konstanter Stärke. Ermüdung, erste Gruppe: Ausfalle einzelner Fasern, später zeitweiliger totaler Ausfall des ganzen Bündels. 4. Kleines Bündel, indirekt gereizt mit konstanter Frequenz von Schwellenreizen. Ausfall des ganzen Bündels durch Ermüdung, keine Abstufung möglich, da die Reize Schwellenwert haben. 5. Muskelfaserbündel; die obere Kurve entspricht der Reizstärke, linke Seite, indirekte Reizung: Abstufungen lediglich durch Zahl der Fasern, für welche die gegebene Reizstärke überschwellig ist. Später Ermüdung nach Massgabe des Ausfalles einzelner Fasern, bis zu einem Minimum. Weiter rechts: direkte Reizung. Weder in dem geringfügigen Anstieg noch in der langdauernden Ermüdungsperiode Alles- oder Nichtsverhalten. 6. Reaktion eines Bündels auf indirekte Reize mit konstant zunehmender Stärke (die obere Kurve gibt diese an): Treppenförmiger Anstieg des Reizerfolges durch zunehmende Anzahl gereizter Fasern. Verminderung der jeweiligen gemessenen Spannung durch Ermüdung, wieder nach Massgabe der durch Ermüdung ausfallenden Fasern: Alles- oder Nichtsgesetz. (Nach Asmussen)

Nervenleitung ist dahingegen ein Kettenprozess: der Reiz löst im gereizten Stück des Nerven einen Prozess aus. Dieser löst im darauf folgenden Sektor des Nerven einen gleichen Prozess aus, u.s.w., aber jeder Sektor liefert an Erregungsquantität soviel, als er zu erzeugen imstande ist: nicht die Stärke des wirksamen Reizes, sondern die Leistungsfähigkeit (die „Ladung") jedes Streckenteils des Nerven bestimmt das Ausmass der Erregung. Zur Erläuterung diente seinerzeit das folgende Bild: ein aus Schiesspulver bestehender Faden, der an einem Ende entzündet wird. Macht man diesen Faden etwa in der Mitte feucht, so ist die Verbrennung im feuchten Teil zwar stark vermindert und verzögert, sie stellt sich aber im darauf folgenden trockenen Teil wieder vollkommen her. So beträgt sich der Nerv, der in einem mittleren Abschnitt durch eine Narkosekammer geht: die Muskelverkürzung bleibt normal, bis sie mehr oder weniger plötzlich vollkommen aufhört, d.h. der Nerv produziert an Erregung „Alles oder Nichts". Dieses „Alles oder Nichts" gilt auch für die Endplatte der Muskelfaser, nicht für die Muskelfaser selbst, d.h. bei direkter Reizung (Technik siehe fig. 5 und Erklärung hiervon). Bei indirekter Reizung gibt die einzelne Muskelfaser bei beliebigen Schwankungen des Reizstromes, solange dieser nur überschwellig ist, immer den gleichen Ausschlag (fig. 6, 1). Wenn bei indirekter Reizung die einzelne Faser ermüdet wird, so bleibt plötzlich jede Kontraktion aus. Bündel von wenigen Muskelfasern, die man mit Strömen von verschiedener Stärke indirekt reizt, können die verschiedenen Reizstärken in soviel Stufen durch entsprechende Kontraktionshöhen (Spannungsgrade) beantworten, als das Bündel Fasern enthält. Bei verschiedener Reizschwelle der einzelnen Nervenfasern, nimmt mit zunehmender Reizstärke die Zahl der erregten Muskelfasern zu und dementsprechend die Spannung. Der Zahl der Fasern entsprechen

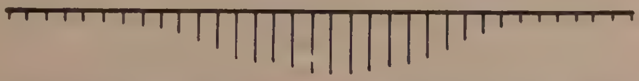


Fig. 7. Eine isolierte Faser, direkt gereizt; Reizgrösse zunehmend sodann abnehmend: Entsprechende Zunahme und Abnahme der Spannung, welche in der Faser auftritt. Dieselbe Faser indirekt gereizt, ebenfalls mit zunehmender Reizstärke, erzeugt immer die gleiche Spannung, die durch Ermüdung im Laufe des Versuches ein wenig abnimmt. (Nach ASMUSSEN und LINDHARD)

auch die Ermüdungsstufen (Verschiedene Kurven auf fig. 6). Die einzelne Faser, mit verschiedenen Stromstärken direkt gereizt, gibt dahingegen beliebig viel Abstufungen (fig. 7) sowohl der Kontraktion als auch der Ermüdung (fig. 6, 5 rechts). Dass die Ermüdung mit Alles- oder Nichts-Effekt in der Endplatte Ihren Sitz hat, zeigt sich dadurch, dass, wenn nach indirekter Reizung Ermüdung aufgetreten ist und der Muskel nicht mehr antwortet, direkte Reizung wieder vollen Effekt hat (fig. 6, 5 Übergang vom linken zum rechten Kurventeil). Bei der geringen Ermüdbarkeit der Nerven bleibt also nur die Endplatte als Sitz dieser Ermüdbarkeit übrig.

Dauertetanus oder Tetanotonus und die Ermüdbarkeit der Muskelfaser

Für den intakten Organismus gibt es nur indirekte Reizung. Die Abstufung, welche die Faser selbst liefern kann, spielt biologisch daher keine Rolle. Dahingegen ist die Ermüdbarkeit der Endplatte stets von grosser Bedeutung. Bei Dauertetanus des ganzen Muskels oder von Faserbündeln fallen ständig Fasern hierdurch aus; sie werden aber durch andere ausgeruhte Fasern ersetzt. Dies hat schon Sherrington eingesehen. Asmussen (1934) hat einen vollgültigen Beweis für die Richtigkeit dieser Lehre geliefert (fig. 8). Der ganze Muskel ist durch diesen Wechsel der Tätigkeitsträger eines minutenlangen Dauertetanus fähig, die einzelne Faser dahingegen verkehrt nur Sekunden lang in diesem Zustand, bleibt dann eine Zeitlang in Ruhe, um hiernach bei kontinuierlicher Reizung wieder einige Sekunden verkürzt zu bleiben.

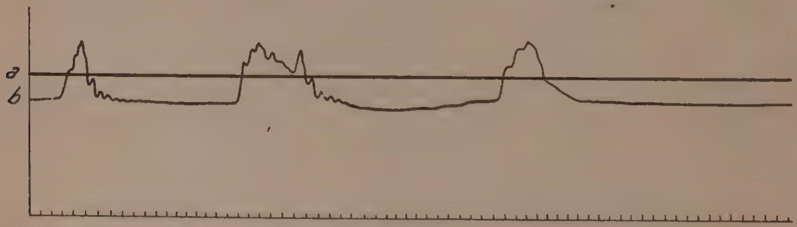


Fig. 8. *a.* Spannung eines ganzen Muskels, *b.* Spannung einer isolierten Muskelfaser, beide bei konstanter indirekter faradischer Reizung. Die einzelne Faser schaltet sich durch Ermüdung und Erholung periodisch aus und ein. Der ganze Muskel gibt kontinuierlichen Tetanus, da für jede zeitweilig ausgeschaltete Faser eine andere einspringt. (Nach Asmussen)

Die spannungslose Kontraktion als Beweis dafür, dass erhöhte Wärmeproduktion und erhöhter Sauerstoffverbrauch keine notwendige Folgen der Reizung sind

Bis vor kurzem sah man in den verschiedenen chemischen Prozessen, die sich im Muskel nach Reizung abspielen, die Ursachen für die Kontraktionsphasen: Kontraktion, Erschlaffung, Wiederherstellung, mit ihrer charakteristischen Wärmeproduktion und ihrem Mehrverbrauch an Sauerstoff. Man meinte, dass jede Reizung den genannten Chemismus in allen gereizten Fasern zur Folge habe, und dass somit durch jede Reizung Wärme und Spannung erzeugt würde. Man stand noch unter dem Einfluss der Meinung, dass die durch die besprochenen chemischen Prozesse entstehende Milchsäure durch Erhöhung des Quellungsvermögens der Muskelkolloide, die Kontraktion verursache und erkläre. Man wusste noch nicht, dass, wenn die Milchsäure sich bildet, die Verkürzung schon vollkommen abgelaufen ist. Einen weiteren Beitrag zur Widerlegung der früheren Auffassung lieferte die Untersuchung der spannungslosen Kontraktion. Selbst die Erzeugung potentieller Energie (Spannung) ist keine direkte Folge des Reizes. Ein kleiner Muskel von Rana schwimmt in Ringerlösung, sodass er sein eigenes Gewicht nicht unter entsprechender Streckung zu tragen hat. Dieser Muskel wird durch eine Serie indirekter elektrischer Reize gereizt. Er kann keine mechanische Energie hervorbringen, weil seine Bewegungen nirgends Widerstand finden. Er kann sich auch nicht wirklich zusammenziehen, weil er vor der Reizung keine dem Ruhezustand entsprechende Gleichgewichtslänge hatte. Er verharrt bei seiner Länge (abgesehen von einer geringfügigen Formveränderung beim ersten Stromstoss der faradischen Reizung). Es tritt keine Spannung, also keine potentielle Energie auf. Die Folge davon ist, dass die Reizung überhaupt nicht durch Wärmeentwicklung, (fig. 9) noch durch gesteigerten Sauerstoffverbrauch gefolgt wird. Auch tritt keinerlei Ermüdung des Muskels auf. Dies ergibt sich aus folgendem Versuch: Ein Muskel, der eine Zeitlang spannungslos gereizt wurde, wird sodann mit dem gleichnamigen Muskel des gleichen Tieres mit Last gereizt. Er ermüdet nunmehr nicht schneller als der lediglich mit Last gereizte Muskel. Die spannungslose Verkürzung entbehrt daher aller

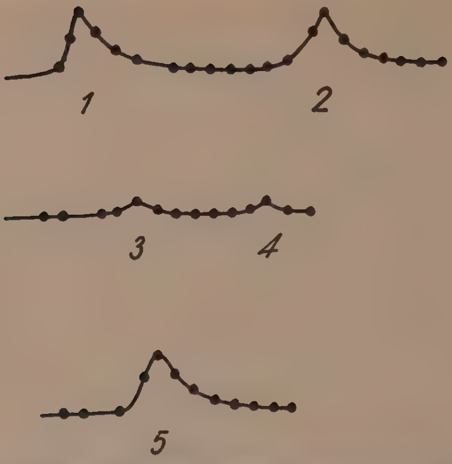


Fig. 9. Totale Wärmeproduktion eines Froschmuskels; die Ordinaten (Wärme) in willkürlichen Einheiten. 1 und 2 isometrischer Tetanus; 3 und 4 *spannungslose Verkürzung;* 5 isometrischer Tetanus, wie 1 und 2. Die geringe Wärmeproduktion in Kurve 3 und 4 ist dem Umstande zuzuschreiben, dass es experimentell nicht gelingt, die Kontraktion volkommen spannungslos stattfinden zu lassen.

irreversibeler Prozesse, die unter Wärmeverlust auftreten, und die man als indirekter Folge der Reizung aufgefasst hatte. Daher muss die in der Tat freiwerdende Energie nach Reizung ohne Last, ein Teil eines cyclischen Prozesses sein, dessen letzte Phase die Wiederherstellung von Reiz- und Verkürzungspotential ist. Denn, da kaum Extrawärme bei spannungsloser Kontraktion auftritt, ist auch keine nutzlose Energie als Wärme verflüchtigt worden. Primär stellt der Muskel lediglich mechanisch brauchbare Energie zur Verfügung, dadurch, dass seine Gleichgewichtslänge sich verändert. Diese Veränderung der Gleichgewichtslänge ist die einzige mechanische Folge der Reizung. Alle Arbeit, Spannungsentwicklung u.s.w. sind sekundäre Folgen von äusseren Kräften, die sich der Annahme der neuen Gleichgewichtslänge widersetzen.

Mizelläre Auffassung der Kontraktion

Den Myosinmolekülen wird Spiralform zugeschrieben (W. T. Astbury 1936). Sie bilden Mizellen, die aus langen biegsamen, aber mit einander fest verbundenen Molekülketten bestehen. Diese haben einen Durchmesser von 10 Å und eine Länge von mindestens 500 Å. In der Ruhe ist Myosin selbst doppelbrechend, eine Eigenschaft, die für die Anisotropie der entsprechenden Muskelfaserschichten verantwortlich ist. Ausserordentlich wichtig für die neueren Auffassungen der Muskelkontraktion ist, dass die Molekülketten im nicht gereizten Muskel sich nicht in einem Gleichgewichtszustande befinden. Sie befinden sich in einem elektrischen Feld, wodurch sie dauernd in gedehntem Zustande erhalten werden. Hierbei sind sie nicht maximal gedehnt, denn sonst würden alle Dehnungsversuche die molekuläre Struktur zerstören. Dass aber die spiralförmigen Moleküle in der Ruhe nicht völlig aufgerollt sind, ergibt sich aus der Tatsache, dass sie kontraktil sind, sie sind also halb aufgerollt. Durch die elektrostatische Dehnung bleiben die Mizellen der die A-Schichten bildenden anisotropischen Stäbchen geordnet. Verschwindet das elektrische Feld, so verliert sich die Ordnung der Mizellen.

Der eigentliche Tonus

Die Folge des genannten elektrostatischen Zustandes ist, dass es neben dem besprochenen Tetanotonus, mit seinen wechselnden Trägern, auch einen vollkommen dauerhaften Tonus geben muss, der rein elektrostatisch unterhalten wird. Der echte Tonus wird durch das elektrische Ruhefeld erzeugt, der die Muskeln zwingt, länger zu sein, als mit ihrer Gleichgewichtslänge übereinstimmt. Dadurch aber wird die Spannung unterhalten, die wir Tonus nennen.

Wie dieser rein statische Tonus vom Zentralnervensystem aus unterhalten und reguliert werden kann, ist eine Frage, die experimentell noch nicht gelöst ist. Ebensowenig ist die Energetik des in der Ruhe dauernd unterhaltenen elektrischen Feldes bekannt. Hier sei erwähnt, dass nach den Erfahrungen des Utrechter Instituts für vergleichende Physiologie der Tonus glatter Muskeln vieler Wirbelloser durch die Viskosität des kolloidalen Muskelsystems unterhalten wird. Diese Viskosität fixiert irgend einen Verkürzungsgrad (das Tonusniveau) wie eine Bremse. Die Kraft dieser Bremse (der Tonusspiegel und dadurch, bei Belastung des Muskels, auch das Tonusniveau) wird in der Tat durch das Nervensystem genau reguliert.

Die eigentliche Muskelverkürzung

Versuche haben gezeigt, dass bei Reizung das oscillographisch (elektrostatisch) messbare elektrische Feld schwächer wird oder verschwindet. Dies kann eine ausreichende Erklärung für die Kontraktion sein: die Riesenmoleküle werden nicht länger gestreckt erhalten, die Spannung muss daher Verkürzung erzeugen. Nach kurzer Zeit stellt sich das elektrische Feld wieder her, wodurch die Fasern wieder länger werden und neuerlich Ruhespannung entsteht. Man kann die beiden Zustände: Ruhe in Spannung, und Kontraktion, welche die Spannung verbraucht, mit analogen Zuständen von vulkanisiertem Kautschuk vergleichen. 1. In der Ruhe ist die Muskelfaser zu vergleichen mit gedehntem Kautschuk. Beim Muskel sind es elastische und elektrostatische Kräfte, die diesen Zustand fixieren. 2. Bei maximaler Kontraktion ist der Muskel mit „ruhendem" Kautschuk zu vergleichen, in welchem die Molekülketten aufgerollt sind. Allein dieser Zustand ist beim Muskel nicht stabil. Der Ursprung des elektrischen Feldes innerhalb der Muskelfaser ist nicht bekannt. Ionenproduktion, Ionentausch an Grenzflächen, vermutlich an den Z-Membranen, dürften als Ursachen für den gemessenen Potentialsprung auftreten. Die Bedeutung der Z-Membranen ergibt sich aus dem Folgenden.

Der elektrische Widerstand der Muskelfaser in ihre Längsrichtung und ihre Veränderung bei Reizung.

(F. Buchthal, 1934–35)

Der Widerstand der Muskelfaser in der Längsrichtung ist sehr hoch. Bei einer solchen Faser mit einem Durchmesser von 70 μ und bei einem Elektrodenabstand von 400 μ beträgt er 3 megOhm (3.000.000 Ohm). Eine Säule von Kochsalzlösung zu 0.6% hat bei gleichen Ausmassen einen Widerstand von 100.000 Ohm. Der spezifische Widerstand der ruhenden Muskelfaser ist 3.000 Ohm/cm, von Kochsalzlösung nur 109 Ohm/cm. Wenn nun nach Reizung das Ruhepotential plötzlich um 1 à 3 mV sinkt, dann sinkt auch der Widerstand um 30 à 50%, um sich in 4 bis 8 sec zum ursprünglichen Werte wiederherzustellen (Fig. 10).

Die Ursache hiervon ist offenbar eine Veränderung in der Ionenpermeabilität und der Ionenkonzentration an Grenzmembranen, für welche die Z-Membranen in Frage kommen. Die Dynamik der Erscheinung ergibt sich aus der Tatsache, dass das Faserpotential mit der Temperatur steigt und sinkt, bis hinauf zu einer Temperatur von 26–28° C. (Buchthal und Lindhard 1936).

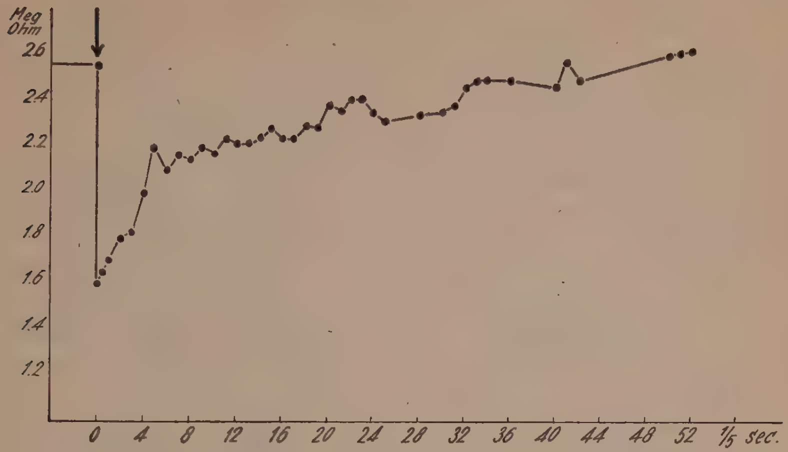


Fig. 10. Veränderung des elektrischen Widerstandes in einer einzelnen Muskelfaser nach Reizung. Abszissen: Zeit in 1/5 Sekunden. Der Pfeil deutet den Zeitpunkt der Reizung an. Ordinaten: Widerstand der Faser. (Nach Buchthal)

Ein Modell für ein Myosinmolekül (nach F. Buchthal 1942, fig 11A und B)

Die Struktur eines Myosinmoleküls muss so sein, dass ein elektrisches Feld einen Einfluss darauf ausüben kann, und in zweiter Linie so, dass innerhalb des Moleküls Anziehung und Abstossung zwischen verschiedenen atomären Bindungen stattfinden kann. Scheinbar ist hierfür ein einfaches Zickzackmodell ausreichend, bei welchem die Aminosäuren der Ketten jeweils eine Ecke mit bestimmtem Winkel mit einander bilden. In einem solchen zweidimensionalen Modelle unterscheiden wir links und rechts je eine Reihe von Eckpunkten, die wir links a und rechts b ernennen wollen; alle a-Punkte seien negativ, alle b-Punkte positiv geladen (fig. 11, A). Benachbarte Punkte würden einander abstossen, sodass dieses Modell sich so weit wie möglich strecken müsste. Dagegen ziehen a- und b-punkte einander an, und hierdurch würde ein solches Molekül so starke Neigung haben sich zu rollen, Spiralform anzunehmen, dass offenbar ein solches zweidimensionales Modell unzureichend ist, da das entsprechende Molekül nicht bestehen kann. Das einfachste Modell ist also ein spiralförmig gerolltes Molekül, mit mindestens 3 Reihen von Eckpunkten, die wir a, b und c nennen

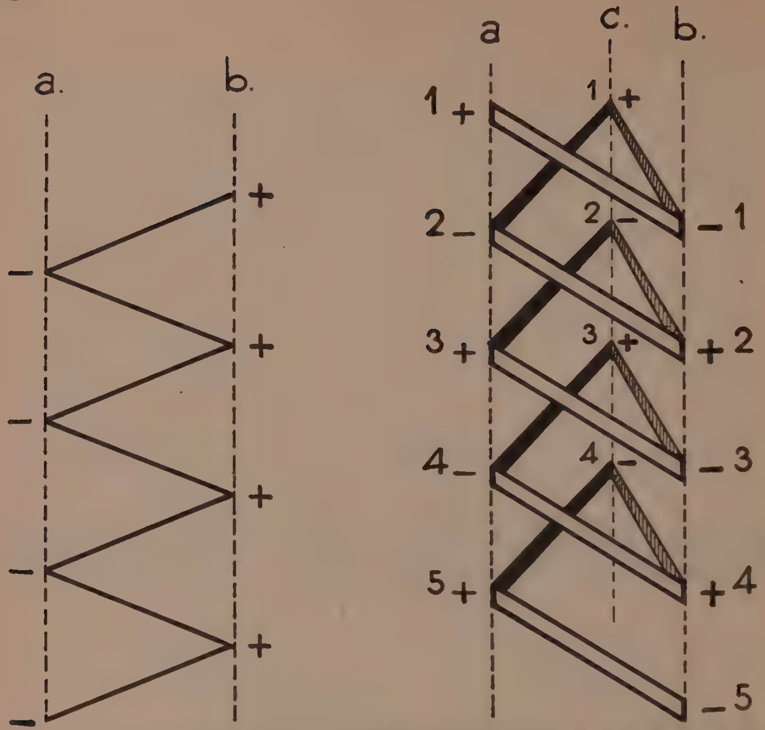


Fig. 11. A. Zickzackmolekül mit zwei Ladungsserien *a* und *b*. B. Spiralförmig gerollte Molekülkette mit drei Ladungsserien *a*, b und *c*. (Nach F. Buchthal)

wollen. Da das spiralförmige Aufrollen durch entgegengesetzte Ladungen entstanden ist, müssen jetzt die Ladungen gleichnamiger Punkte in den drei Reihen abwechselnd positiv und negativ sein (fig. 11 B).

In der folgenden Auseinandersetzung beschränken wir unsere Aufmerksamkeit auf Punkt a_1 mit positiver Ladung. Auf diesen Punkt üben alle benachbarten Punkte, je nach ihrer Ladung und Entfernung, Einfluss aus. a_1 wird in der Längsrichtung durch a_2 angezogen, und in geringerem Masse durch a_3 abgestossen; a_1 wird weiterhin (wenn auch in anderer Richtung) abgestossen von c_1 und b_2 u.s.w. Die Entfernung der Punkte voneinander, die durch die besprochene Feldwirkung oder experimentell verursachte Dehnung verändert werden kann, muss auf die Kontraktion einen grossen Einfluss haben. Befand sich der ruhende Muskel im Zustand geringster Länge, so muss die Anziehung zwischen benachbarten Punkten in der Längsrichtung überwiegen. Dehnung der Muskelfaser muss dahingegen durch Vergrösserung des in Frage stehenden Abstandes diese Anziehung vermindern. BUCHTHAL vergleicht dieses Modell mit seinen geladenen Eckpunkten mit einem Kondensator und bedient sich zur Ableitung seiner Theorie der bekannten Formel $E = C.V$, wobei E die Ladung, C die Kapazität und V die Spannung ist. Die Ladung E ist konstant. Die Kapazität ist umgekehrt proportional dem Abstand zwischen den entgegengesetzt geladenen Punkten („Kondensatorplatten"). Bei zunehmendem Abstand, wenn also C kleiner wird, muss die Spannung V grösser werden, da ja E konstant ist. Bei kleinerem Abstand und daher grösserem C muss V kleiner werden. Hiernach kann man sich die Verkürzung als folgt vorstellen: Durch äusseren Einfluss möge der Abstand zwischen a_1+ und a_2- kleiner werden. Hierdurch kann der Potentialsprung zwischen a_1 und a_2 in geringerem Masse nach Aussen wirken (stärkere gegenseitige Bindung). Die Kapazität aber nimmt zu, da in a_1 eine teilweise Kompensation der positiven Ladung, was ihre Wirkung nach aussen betrifft, stattfindet, in a_2 eine entsprechende Verminderung der negativen Ladung. Durch Influenz wird ein Teil dieser Wirkungs- oder Feldveränderung auf b_1 und b_2 übertragen. Hierdurch steigt der Potentialsprung zwichen b_1 und b_2, sodass das Anziehungsvermögen zwischen beiden Punkten zunimmt: sie bewegen sich auf einander zu. Etwas entsprechendes geschieht zwischen c_1 und c_2. Dieser Prozess pflanzt sich über die ganze Länge der Spirale fort, es sei denn, dass er durch Streckung der Faser aufgehalten wird und zwar naturgemäss da, wo die Entfernung zwischen den Eckpunkten zu gross geworden ist. Diese Ecken können an der Kontraktion nicht teilnehmen. Bei spannungsloser Kontraktion, wo von solch eine Entfernung keine Rede sein kann, werden immer alle Punkte der Ketten an der Kontraktion teilnehmen. Es sei hier unter allem Vorbehalt auf eine Möglichkeit hingewiesen: es fällt immer noch schwer sich ein deutliches Bild der weitergehenden Kontraktion bei Tetanus, verglichen mit der maximalen Kontraktion bei Einzelreizen zu machen. Es bleibt bei jedem Reiz in der Muskelfaser etwas übrig, was sich zu dem folgenden Reizeffekt summiert. Wirklich befriedigend ist diese Erklärung an sich nicht. Bei BUCHTHAL's Modell könnte man daran denken, dass bei jedem Reiz die genannten Eckpunkte einander näher kommen, und die Anziehung zwischen benachbarten Punkte desto grösser wird, je näher sie einander durch vorhergehende Reize gebracht worden waren. Dies könnte auch für den isometrischen Tetanus gelten, bei welchem ja die anisotrope Substanz auf Kosten der isotropen kürzer wird. Die Bedeutung des Abstandes zwischen zwei Punkten, die einander zum Zwecke der Kontraktion anziehen müssen, ergibt sich aus dem folgenden Versuch: Wenn man eine Muskelfaser dehnt, entsteht Spannung. Wenn man sie reizt, entsteht unter isometrischen Bedingungen auch Spannung. Man kann beide spannungerzeugenden Einflüsse kombinieren, und zwar auf zweierlei Weise. Man kann erst dehnen und dann reizen (wir nennen die Spannungszunahme durch Reizung Extraspannung). Man kann aber auch erst reizen und dann dehnen. Im letzteren Falle wird maximale Dehnung der schon verkürzten Faser eine höhere Spannung zuwegebringen als wenn man erst dehnt und dann reizt, in welch letzterem Falle eine geringe Extraspannung zu messen ist. BUCHTHAL erklärt dies so, dass vorhergehende passive Dehnung die Eckpunkte voneinander entfernt hat, wodurch die Erzeugung der Extraspannung geschädigt wurde.

Alle diese Ableitungen beschränken sich auf die anisotropen Schichten. Das Verhalten der isotropen Schichten wird durch unser Modell nicht beschrieben. Ihre Gleichgewichtslängen veränderen sich nicht. Dies kommt vor allem daher, dass in den anisotropen Schichten die Moleküle geordnet sind, in den isotropen Schichten dagegen nicht, darum zeigen diese auch keine Doppelbrechung. Die Kontraktion der Fasern hat zur Voraussetzung, dass in den kontraktilen Elementen die Mizellen geordnet sind. Wo, wie in den isotropen Schichten, die Mizellen chaotisch durcheinander liegen, kann eine Kontraktion dieser Mizellen nur die sogenannte Steifheit erhöhen; d.h. das Verhältnis Spannungszuwachs zu Längenzuwachs $(\frac{\Delta \text{ Spannung}}{\Delta \text{ Länge}})$ erhält einen grösseren Wert. Dies ist wichtig für die Übertragung des mechanischen Effektes der Kontraktion in den anisotropen Schichten auf den ganzen Muskel mit seinen Sehnen.

II. Die thermoelastische Theorie der Muskelkontraktion nach U. EBBECKE und H. REMBERG. (1938)

Als Modell für diese Theorie dienen Fäden von mässig vulkanisiertem Kautschuk. Bei diesen kann man folgende thermoelastische Erscheinungen feststellen. *a.* Wenn ein solcher Faden durch Anhängen eines Gewichtes gedehnt wird, tritt in der ersten Phase dieser Dehnung Abkühlung auf. Man kann dies dadurch verdeutlichen, dass man den Kautschuk mit einem Kristall vergleicht. Beim Einsetzen der Dehnung werden offenbar molekuläre oder intramolekuläre Bindungen gebrochen, sodass man diese Erscheinung mit der Lösung von Kristallen oder dem Schmelzen von Eis vergleichen kann. Wenn die Dehnung weiter geht, beginnt der umgekehrte Prozess: es wird von dem Kautschuk Wärme abgegeben, deren Entstehung dadurch zu erklären ist, dass die Kautschukmizellen parallel zueinander zu liegen kommen (Gleichrichtung unter Entstehung von Doppelbrechung). Hierdurch erhöht sich ihre gegenseitige Anziehung, sodass sich kristalähnliche Verbindungen bilden. Die abgegebene Wärme könnte dann als eine Art Kristallisationswärme aufgefasst werden. Im Zustand einer gewissen Dehnung hat nun Erwärmung von aussen her (der Kautschukstreifen befindet sich in einer Röhre, die Erwärmung oder Abkühlung ermöglicht) sehr ausgesprochene Verkürzung zur Folge. Die Wärmeabgabe bei weitgehender Dehnung entspricht also Verkürzung bei Hinzufügung von Wärme (Demonstration auf dem internationalen Physiologenkongress 1938 zu Zürich). Ein ähnlicher Versuch war den Kautschuktechnikern unter dem Namen „Schrumpfeffekt" schon lange bekannt. Wenn man hinreichend gekühlten Kautschuk schnell und kräftig dehnt, so tritt plötzlich ein sehr grosser Widerstand gegen Dehnung auf, den man „Verfestigung" nennt. In diesem Zustand haben sich die parallell gerichteten Mizellen miteinander verbunden, sodass man sie nun nicht weiter auseinanderziehen kann. So lange der Kautschuk kalt bleibt, behauptet er diese Länge. Bringt man ihn dagegen in warmes Wasser, so tritt heftige Kontraktion auf. Durch die Dehnung ist Spannung entstanden. Durch die Verfestigung konnte sie sich nicht ausgleichen. Durch die Erwärmung, d.h. die Bewegung der Mizellen, machen diese sich voneinander los und können nun frei ihre Spannung durch Verkürzung ausgleichen. Wie bei der Muskelverkürzung geht auch beim Schrumpfeffekt die Anisotropie verloren. Beim Kautschuk wie beim Muskel bedeutet daher Ruhe: Ordnung, zu vergleichen mit der Ordnung der Ionen in einem Kristall. Kautschuk und Muskel müssen nach dieser Theorie vor dem Auftreten der Kontraktion Spannung haben. Darin stimmt die Theorie von

Ebbecke mit derjenigen von Buchthal überein. Der Prozess der Kontraktion ist reversibel, denn wenn man in dem Versuch von Ebbecke den Kautschukstreifen wieder abkühlt, dann tritt Erschlaffung auf, der Kautschuk gibt der Last nach.

Zahlreiche Eigenschaften und Erscheinungen des Modells kann man beim Muskel zurückfinden. Der Kautschuk, zumal dünne Fäden, sind imstande schnelle Zuckungen auszuführen von 0.1 sec. Auch unvollkommener und vollkommener Tetanus ist bei Kautschuk zu erzielen. Ähnlich wie in Buchthal's Theorie erzeugt die Reizung nicht eigentlich Energie. Die Verkürzung macht Gebrauch von der Aufhebung der molekulären Ordnung, die durch die Vordehnung zuwege gebracht wurde und weiterhin von der potentiellen Energie, welche als Spannung durch die Vordehnung erzeugt worden war. Die Ursache der Ruhespannung im Muskel ist nicht bekannt.

III. Chemische Verkürzungstheorie von A. Szent-Györgyi und seinen Mitarbeitern (1940–42)

Die Eiweissart, die der Hauptsache nach die Muskellfaser bildet, trägt den Namen Myosin. Myosin ist diejenige Eiweissfraktion des Muskels, welche aus diesem durch eine Lösung von 0.6 mol KCl bei pH 8.5 à 9 extrahiert wird und die bei pH 7, wenn man die KCl-Lösung bis zu einer Konzentration von 0.1 mol verdünnt, praecipitiert. Bei derartigen Extraktionen tritt Myosin in zwei Modifikationen auf, die wir zunächst Myosin A und Myosin B nennen. Myosin A findet man in Extrakten, bei denen man die Flüssigkeit zwanzig Minuten lang auf dem zu extrahierenden Muskelbrei hat stehen lassen. Myosin B dahingegen entsteht dann, wenn man den Extrakt längere Zeit z.B. 24 Stunden, auf dem Muskelbrei stehen lässt. Hierbei tritt Gelbildung auf, das Gel löst sich jedoch bei Hinzufügung von Adenyltriphosphat (ATP). Myosin B, das offenbar aus A entsteht, zeichnet sich durch grössere Molekülaggregate, also durch höhere Viskosität von diesem aus. Durch Einspritzen von Myosin in Flüssigkeiten (Salzlösungen) kann man Fäden von diesem Stoff erhalten, sowohl von A als von B und mit diesen Fäden kann man experimentieren. Auf überraschende Weise zeigen diese Myosinfäden ein Verkürzungsvermögen, welches mit demjenigen der Muskelfasern verglichen werden kann (Fig. 12).

1. Fäden aus Myosin B kommen in Muskelextrakt und wer-

den mit dem Mikroskop beobachtet. Innerhalb 30 Sekunden ziehen sich dickere Fäden zusammen, sodass sie nur mehr ein Drittel ihrer ursprünglichen Länge haben. Gleichzeitig wird solch ein Faden dünner, dunkel und undurchsichtig. Die Kontraktion geht noch 2–3 Minuten lang weiter und erreicht eine Längenverminderung um 66%. Die Tatsache, dass der Faden kürzer und zugleich dünner wird, unterscheidet diese Kontraktion von der anisodiametrischen Verkürzung der Muskelfasern. Dünne Myosin B Fäden ziehen sich schneller zusammen als dicke. Dies ergibt sich aus Tabelle 3.

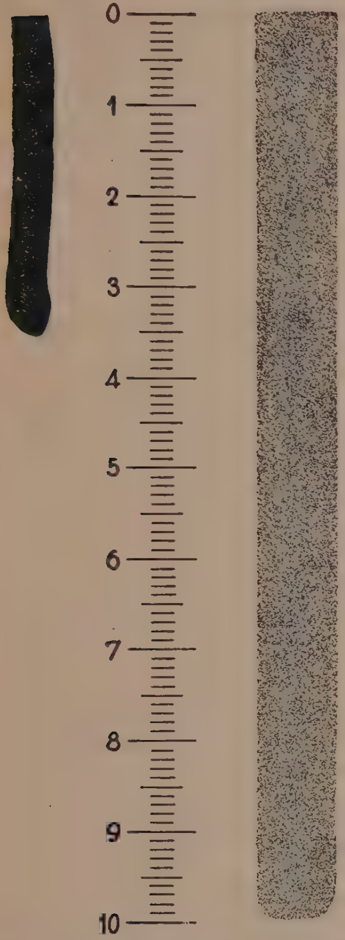


Fig. 12. Rechts sieht man einen Myosinfaden (Myosin B oder Aktomyosin). Links: Der gleiche Faden kommt in einen Extrakt aus Kaninchenmuskel in Wasser. Es tritt heftige Kontraktion auf, die unter dem Mikroskop beobachtet wird. Der Faden wird viel kürzer (seine Länge beträgt nur noch 1/3 der ursprünglichen Länge) und ziemlich dunkel. (Nach A. SZENT-GYÖRGYI)

TABELLE 3

Dicke der Faser	Verkürzungszeit	Verkürzung in %
0,1 mm	1—2 Min	20—25%
0,05 ,,	¼ Min	36—40%
n μ	n^1 msec	60%

Die geringste Faserdicke und ihre Verkürzungszeit ist nur in ihrer Grössenordnung (n und n^1) angegeben.

Welche Stoffe enthält der Muskelextrakt, durch welche die heftige Kontraktion des Myosin B Fadens erzeugt wird, die aber wenig Einfluss auf Myosin A haben? Bei diesem künstlichen Verkürzungsprozess spielt ATP eine grosse, wenn auch nicht die einzige Rolle, denn der Muskelextrakt darf nicht fehlen. ATP + gekochter Muskelextrakt oder veraschter

Muskelextrakt ruft heftige Kontraktion eines Fadens von Myosin B hervor (fig. 13 a). Das bedeutet, dass ATP + anorganische Stoffe für diesen Vorgang nötig sind. Es hat sich in der Tat gezeigt, dass bestimmte Salze bei der Kontraktion eine Rolle spielen. Eine Kurve, die der auf fig. 13 a abgebildeten entspricht, erhält man nämlich, wenn man zum Myosinfaden ATP gelöst in 0,1 mol KCl + 0,01 à 0,001 mol $MgCl_2$ hinzufügt. ATP + 0,1 mol KCl verursacht nur eine relativ langsame Kontraktion (fig. 13 Kurve b).

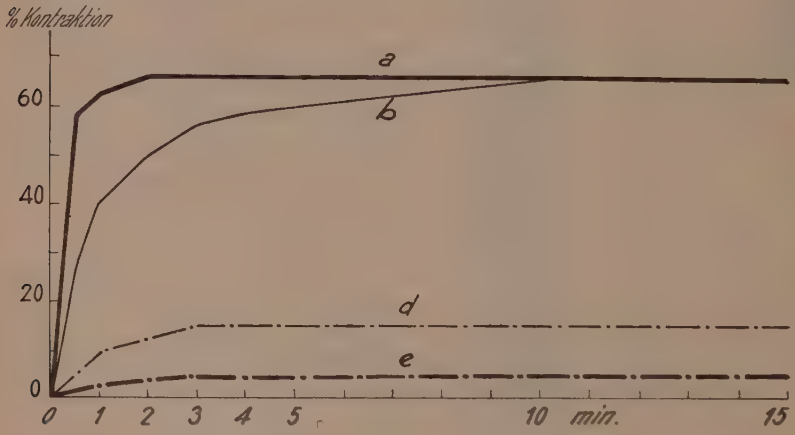


Fig. 13. Kontraktionsformen von Myosin B und Myosin A, durch verschiedene Zutaten. Myosin A in ungereinigtem und in gereinigtem Zustand (zweimal durch Seitzfilter K filtriert). Abszissen: die Zeit, Ordinaten: Kontraktion in % der Fadenlänge. Die Bedeutung der einzelnen Kurven findet man im Text. Kurve c des Originals (gereinigtes Myosin A ohne $MgCl_2$) ist weggelassen; sie liegt nur um ein Geringes höher als Kurve d.

Myosin A, nicht durch ein Seitz–K–Filter filtriert, gibt mit ATP + KCl nur eine schwache langsame Kontraktion. Nach Filtrierung (Entfernung der Verunreinigung mit Myosin B), ergibt sich eine noch niedrigere Kurve (d), die durch $MgCl_2$ nicht verstärkt, sondern unterdrückt wird (Kurve e). In einer etwas älteren Reihe von Publikationen (1940) aus dem Institut von A. SZENT-GYÖRGYI veröffentlicht dieser Forscher, im Verein mit einer Reihe seiner Mitarbeiter, Ergebnisse über die Bedeutung von Kalium für die Muskelkontraktion. Nach E. ERNST und FRICKER (1934) ist Kalium im ruhenden Muskel in gebundenem Zustand anwesend und wird bei der Kontraktion frei gemacht.

Nach seiner Befreiung ionisiert das Kalium, was sich durch „Volumkontraktion'' zu erkennen gibt (E. Ernst 1925). Denn Ionen binden das Wasser so, dass das Volumen des wässerigen Systems des Muskels kleiner wird. Dass es sich hierbei um Kalium und nicht (was auch möglich wäre), um Phosphor handelt, ergab sich aus Versuchen von E. Ernst und E. Mórocz (1940). Veratrin verlängert, wie bekannt, den Prozess der Muskelkontraktion und zwar dadurch, dass der „Grundprozess'' der Muskelkontraktion länger dauert als beim normalen Muskel. Und gerade dieser „Grundprozess'' hat es mit Kalium zu tun. Denn der durch Veratrin vergiftete Muskel gibt während seiner Verkürzung mehr Kalium an eine Durchströmungsflüssigkeit ab, als der normale Muskel. Während der längeren Dauer der Veratrinkontraktion wird das ionisierte Kalium abnormal lang festgehalten, was sich durch lang anhaltende Volumkontraktion zu erkennen gibt. Durch dieses Zusammengehen von Ionisierung des Kaliums mit der Kontraktion ergibt sich, dass die K-Ionen als sehr wichtige Faktoren der Kontraktion anzusehen sind. Bei der Erschlaffung verschwindet das ionisierte Kalium.

2. Myosinfaden und Muskel. Um die Frage zu beantworten, ob die Myosinkontraktion etwas mit der natürlichen Muskelkontraktion gemein hat, wird eine kleine Gruppe von Muskelfasern derart mit destilliertem Wasser und durch Gefrieren behandelt, dass seine normale Struktur vernichtet wird und jegliche natürliche Kontraktilität hierdurch verschwindet. Ein 2 mm breiter Streifen von einem Kaninchenmuskel wird parallel zur Faserrichtung ausgeschnitten, eine Zeitlang in destilliertem Wasser belassen, sodann auf dem Gefriermikrotom festgefroren und hieraus werden Schnitte von der Dicke einer Muskelfaser und in der Richtung des Faserverlaufes angefertigt. Derartige Präparate kommen in einer Lösung von 0.1 mol KCl unter das Mikroskop. Ihr Verhalten bei Hinzufügung derjeniger Substanzen, die vermutlich für die Myosinfadenkontraktion verantwortlich sind, wird mit Hülfe eines Okularmikrometers festgestellt. Sobald man zu diesen Präparaten einen Tropfen einer ATP-Lösung fügt, tritt heftige Verkürzung der Muskelfasern auf und zwar bei gespannten gedehnten Fasern um 50–60%. Es verhält sich daher das Myosin der Muskelfasern wie Myosin B.

3. Myosinsuspensionen (Myosin B). Salze und ATP haben eine Wirkung auf Myosinsuspensionen, die wir weiter unten mit den entsprechenden Wirkungen auf Myosinfäden vergleichen

werden. KCl 0,1 mol verursacht Präzipitierung einer Myosinsuspension, die bei noch geringerer Salzkonzentration noch schneller vor sich geht. Fügt man nun zu dem Gemisch auch noch ATP (z.B. 14 mg %) hinzu, so tritt „Superpräzipitierung" auf, d.h. es entstehen grobe Granula. Der Niederschlag sinkt schnell zu Boden und es bleibt eine klare Flüssigkeit darüber stehen.

Bei höheren Konzentrationen von KCl tritt keine Präzipitierung, sondern Lösung des suspendierten Myosins auf. Bei einer Konzentration von 0,4 mol KCl wird eine Suspension von Myosin B nicht wahrnehmbar aufgelöst. Fügt man aber ATP hinzu, so erfolgt solch eine Lösung. ATP erhöht daher alle die Wirkungen von Salzlösungen, die ihrer jeweiligen Konzentration entsprechen.

Analogie zwischen dem Verhalten von Suspensionen und Myosinfäden

ATP plus KCl bei höherer KCl-Konzentration löst beide auf. ATP plus KCl bei niederer Konzentration verursacht Kontraktion von Myosinfäden und „Superpräzipitierung" von Suspensionen.

Unterschied zwischen beiden Versuchsobjekten

Bei niederer Konzentration bringt Salz an sich Präzipitierung zuwege; niemals aber verursacht eine derartige Salzlösung allein eine Kontraktion des Myosinfadens. Das weist darauf hin, dass Präzipitierung und Superpräzipitierung wesensverschiedene Erscheinungen sind. Salz allein verursacht vermutlich lediglich Aggregation der Myosinmizellen, während Salz plus ATP vielleicht tiefgehende Veränderungen der Mizellen hervorruft, durch welche Superpräzipitierung und im anderen Falle (Myosinfaden) Kontraktion verursacht wird. Für diese Auffassung spricht die Tatsache, dass Salze allein keinen Einfluss auf die Doppelbrechung von Fäden mit orientierten Mizellen haben. Dahingegen bringen Salze mit ATP die Doppelbrechung bei der Fadenverkürzung vollkomen zum Verschwinden, eine Erscheinung, die bekanntlich auch bei sich verkürzenden Muskelfasern auftritt.

Das Wesen von Myosin A und Myosin B. (A. SZENT-GYÖRGYI, S. 67)

Myosin A ist reines Myosin (F. B. STRAUB). Myosin B ist eine stöchiometrische Verbindung von Myosin A mit einem andern Stoff, den der Autor Aktin genannt hat. Daher nennt er nunmehr das Myosin B „Aktomyosin". Myosin tritt in vielerlei Form auf: Als freies Myosin (früher A), als ATP-Myosin, als Aktomyosin (früher B) und als ATP-Aktomyosin. Diese Stoffe haben die folgenden Eigenschaften:

1. Myosin A ist gut in KCl löslich, vermag sich aber nicht zu verkürzen.
2. ATP-Myosin ist weniger löslich in Salzlösungen, dagegen schwach kontraktil bei niederen Salzkonzentrationen.
3. Aktomyosin ist nicht löslich in Salzlösung und nicht kontraktil.
4. ATP-Aktomyosin ist ausserordentlich empfindlich gegenüber den verschiedenen angewandten Salzkonzentrationen.

TABELLE 4

Verhalten der verschiedenen Formen und Verbindungen von Myosin bei verschiedenen Konzentrationen von KCl und konstanter Konzentration von $Mg Cl_2$.

Mol. KCl + 0.01 mol. $MgCl_2$	Myosin	ATP-Myosin	Akto-Myosin	ATP-Akto-Myosin
0	–	–	–	–
0,01–0.19	–	+	–	+++
0,20	–	–	–	?
0,21–0.23	–	–	–	–
0,24–0.31	–	–	–	×
0,32–0.46	×	–	–	×
0,47–0.60	×	×	–	×

– bedeutet inaktiv
× „ gelöst
? „ teilweise kontraktil, teilweise gelöst
+ „ schwache Kontraktion
+++ „ maximale Kontraktion.

Bei verschiedenen KCl-Konzentrationen (unter 0,01 mol und bei 0,21–0,23 mol) und Anwesenheit von 0.001 mol $MgCl_2$ ist ATP-Aktomyosin inaktiv, d.h. nicht löslich und nicht kontraktil (Zeichen – auf der Tabelle); bei 0,01–0,19 mol KCl ist es maximal kontrahiert (Zeichen +++), oder bei wieder höherer Salzkonzentration aufs Neue inaktiv (–) oder gelöst (Zeichen ×). (Nach Versuchen mit Myosinfäden von T. Erdös p. 60, Tabelle 1.)

Anwendung der beschriebenen Tatsachen auf die Muskelphysiologie

Im Muskel ist, beurteilt nach der Löslichkeit, Aktomyosin anwesend. Lebender und frisch zerkleinerter Muskel enthält sehr empfindliches ATP-Aktomyosin. Daher wird man vermutlich zahlreiche Muskelphysiologische Erscheinungen durch geringfügige Veränderung der Ionenkonzentration in der Muskelfaser erklären können. Dabei kann es sich um andere Ionen handeln, als diejenigen, die bei den Versuchen gedient haben: denn auch bei den Versuchen ist die Ionenwirkung nicht spezifisch.

IV. Einige allgemeine Betrachtungen

Man sah eine Zeitlang den Muskel als Glykogenmotor an. ATP sollte lediglich als Phosphordonator dienen, bei der Bereitung des Laktazidogens (Hexosemonophosphorsäure), als Übergang von Glykogen über Methylglyoxal nach Milchsäure und zwar neben dem Phosphagen (Kreatinphosphorsäure). Manche Forscher meinten, dass die auf genannte Weise zustande kommende Phosphorylierung lediglich dazu dienen sollte um die anaerobiotische Milchsäurebildung zu beschleunigen. Elektrische Messungen sowie die Beobachtungen über spannungslose Verkürzung, neben älteren Einwendungen gegen die Versuche, Kontraktion durch einen Chemismus dieser Art zu erklären, zwingen uns die älteren Theorien fallen zu lassen. ATP ist offenbar viel mehr als Phosphordonator und hat direkten Einfluss auf die Verkürzung. Es bestehen mehr Beziehungen zwischen den drei neuen Theorien, als zwischen diesen und den älteren Auffassungen, wenn auch in allen drei neuen Theorien noch zahlreiche empfindliche Lücken vorhanden sind. Veränderungen von Valenzen (Ladungen) des Myosinmoleküls spielen sowohl bei Buchthal als bei Szent-Györgyi eine grosse Rolle. Anziehung und Abstossung werden von Buchthal durch Veränderungen der Feldstärke in den Fasern erklärt. Für Szent-Györgyi ist ein chemischer Faktor verantwortlich für Umladungen, die ihrerseits Aggregation (Verkürzung) und Desaggregation (Erschlaffung) zuwegebringen (Ionisierung von in der Ruhe gebundenem Kalium nach Reizung; die K-Ionen verschwinden bei der Erschlaffung). Bei Ebbecke und Buchthal finden wir das nämliche Problem der Ruhespannung, als Bedingung für die Verkürzung auf Reizung hin. Offenbar denken beide Autoren nicht an die gleiche Ursache dieser Ruhespannung, über die sicherlich noch nicht das letzte Wort gesprochen ist. Uns will scheinen, dass, welche Theorie der Muskelverkürzung sich auch in Zukunft behaupten möge, die ausgedehnten Forschungen der Kopenhager Schule unsere Kenntnis der Muskelphysiologie sehr vertieft haben.

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THE TEGELEN FAUNA, WITH A DESCRIPTION OF NEW REMAINS OF ITS RARE COMPONENTS (LEPTOBOS, ARCHIDISKODON MERIDIONALIS, MACACA, SUS STROZZII)

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The first list of mammals from the Tegelen Clay was published by EUGÈNE DUBOIS in 1904 (*a*, *b*). It runs as follows:

Equus Stenonis Cocchi
Rhinoceros etruscus Falc.
Hippopotamus amphibius L.
Cervus Sedgwickii Falc. (= *Cervus dicranius* Nesti)
Cervus (Axis) rhenanus sp. n.
Cervus (Axis) sp.
Cervus tegulensis sp. n.
Trogontherium Cuvieri Owen.

NEWTON added to these species in 1907 (in REID and REID, 1907), 1908 and 1910:

Microtus (Mimomys) pliocaenicus Major
Microtus (Mimomys) intermedius Newton
Talpa Europaea,

and, in 1913, *Ursus etruscus* Cuvier. Moreover, as the result of his determination of some specimens sent to him by Dr. TESCH, NEWTON mentioned on a label or in a letter:

Hyaena crocuta
Castor fiber L.
Myogale spec.

The Reverend ST. RICHARZ (1921) has recorded:

Elephas meridionalis Nesti
Sus Strozzii Meneghini.

It is regrettable that MAYET et ROMAN (1923), in their comparison of "faunes de Mammifères d'age Villafranchien–Saint-Prestien", still used DUBOIS' primary list, without taking notice of NEWTON's and RICHARZ's important papers. This is the reason, that the French authors place the Tegelen fauna in the Saint-Prestian, an error, which ever since has repeatedly recurred in literature.

Bernsen, in his thesis (1927) on the Rhinos of Tegelen, gave the following list borrowed from Reid and Reid (1915), adding the records by Richarz, and *Hyaena perrieri* which was first mentioned for Tegelen by Dubois (1923) after the determination by the late Dr. J. Metzelaar of the *Hyaena*-tooth in Teylers Museum:

Equus Stenonis Cocchi
Rhinoceros etruscus Falc.
Rhinoceros Mercki Jäger (first recorded by Bernsen)
Sus sp. (*Strozzii* Menegh.? *scrofa* L.?)
Hippopotamus sp. (*major* Cuv.)
Cervus dicranius Nesti
Cervus rhenanus Dub.
Cervus teguliensis Dub.
Elephas meridionalis Nesti
Microtus (Arvicola) pliocaenicus Major
Microtus (Arvicola) intermedius Newton
Castor europaeus L.
Trogontherium Cuvieri Fischer
Talpa europaea L.?
Myogale sp.
Ursus etruscus Cuv. (= *U. arvernensis* Croiz.)
Hyaena Perrieri Croizet
Hyaena crocuta Zimm.

Bernsen (1930–'34), in his Revision of the Tegelen mammals, treated of:

I (1930) *Elephas meridionalis* Nesti, archaic form
II (1931) *Equus stenonis* Cocchi, race *major* Boule
III (1931) *Macacus* cf. *florentinus* Cocchi
IV (1931) *Sus strozzii* Men.
V (1931) *Hyaena perrieri* Cr. et Job.
VI (1932) *Ursus etruscus* Cuv.
VII (1932) *Mustela* spec.
VIII (1932) *Hystrix* cf. *etrusca* Bosco
IX (1933–'34) *Cervidae* (after Bernsen's death, in 1932, arranged by the present authoress).

The result of this revision was, therefore, that *Hippopotamus* and *Hyaena crocuta* had to be struck off the list. The tooth formerly referred to the hippopotamus is one of *Sus strozzii*, and all the teeth of *Hyaena* preserved belong to *Hyaena perrieri*. It is not surprising that *Hippopotamus* did not occur in so old a pleistocene fauna as that of Tegelen. Stehlin (in Stehlin et Dubois, 1932–1933, p. 228, foot-note) wrote: "L'époque de sa plus grande fréquence et diffusion dans les latitudes moyennes ne vient qu'après la limite du Pliocène et du Pléistocène (Tegelen, etc.), et correspond au Pléistocène prérissien", viz. Upper Freshwater Bed, Hauptfauna of Mosbach, Mauer, etc.

Assisted by new finds and after a close comparison with specimens from synchronic localities it is possible now to publish the following list:

Desmana tegelensis Schreuder
Talpa (*praeglacialis* Kormos?)
Hypolagus brachygnatus Kormos
Mimomys pliocaenicus (Major)
Mimomys newtoni Major
Hystrix cf. *etrusca* Bosco
Castor fiber L.
Trogontherium boisvilletti (Laugel)
Pannonictis pilgrimi Kormos
Pannonictis pliocaenica Kormos
Crocuta perrierii (Luroth)
Ursus etruscus Cuvier
Sus strozzii Meneghini
Archidiskodon meridionalis (Nesti), archaic type
Dicerorhinus etruscus (Falconer)
Dicerorhinus merckii (Jäger)
Equus robustus Pomel
Eucladoceros tegulensis (Dubois)
Cervus rhenanus Dubois
Cervus dicranius?
Leptobos cf. *elatus* (Pomel)
Macaca florentina (Cocchi)

Among this faunal assemblage *Trogontherium* is by far the most common of all. The great quantity of remains justifies the term "*Trogontherium*-Tone" used by P. G. Krause for the Tegelen Clay. Allthough neither a complete skeleton, nor a skull has ever been saved, the many fragments represent all the elements of skull and skeleton, so that it is only the length of the vertebral column we do not know. The particular bipartite form and rough surface of the premaxillary beneath the broad nasal opening and the alveoles of the incisors point to a strongly muscular bipartited upper-lip of which both halves were prehensile. This fact, in conjunction with the luxuriance of the water-flora living in the pools and the numerous abandoned channels of the meandrine river-branches of the delta, make it probable that *Trogontherium* lived there as the manatee does among the rich water-flora of the delta of the Amazone and the Orinoco, and which, when swimming, snatches the vegetable food from the surface of the

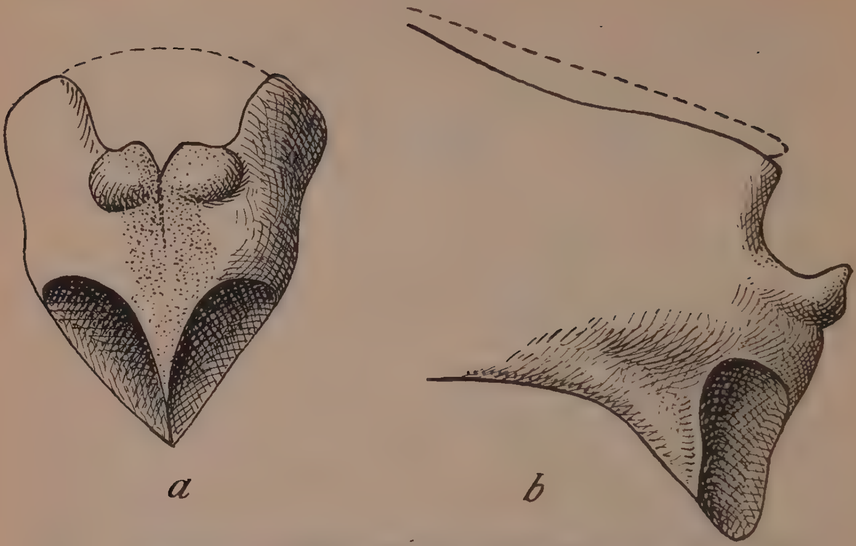

Fig. 1. *Trogontherium boisvilletti*, Tegelen. Premaxillary, nat. size; *a* from the front, *b* right side.

water with its prehensile upper-lips. Reid and Reid (1915) mentioned among the Tegelen flora *Euryale*, now occurring in China, five species of *Potamogeton*, two of *Najas*; furthermore *Trapa natans*, *Sagittaria*, *Alisma*, *Stratiotes*, Water-ranunculus, Water-mint, etc. Perhaps, in winter *Trogontherium* may have had recourse to rhizomes and tubers, and to the bark of trees, which is the favourite food of the beaver throughout the year, although the latter takes some green food in summer, but always feeds on land. This different way of living will have been the reason that *Trogontherium* and *Castor*, both aquatic rodents of about equal size, kept out of eachother's way. For also in the English Forest Bed, in Mosbach and in Jockgrim, they lived side by side, although in all these localities their remains are scanty. Also *Trogontherium*'s much less hypsodont molars, each with three roots, justify the conclusion that its food was softer than the coarse food of the beaver. When during the Pleistocene the climate became rawer and the vegetation poorer, the beaver was able to get through, but the other did not survive the Riss-glaciation. The youngest English deposits in which remains have been found are the "Glacial Drift of Copford" in Essex, and the High-Terrace near Greenhithe, in the Thames Valley, Kent.

Less common than *Trogontherium* are the remains of both deer, but they are nevertheless numerous in the collections. Less common than the deer, but by no means rare are the horse, and both species of *Dicerorhinus*.

Their remains being so small, as a rule the Micromammalia escape the attention of the workmen, but neither the voles nor the mole will have been rare in the fauna of Tegelen. The Tegelen Desman lived on the rich waterfauna (insects, molluscs, crustaceans, small fishes and frogs), which it snatched from the plants and from the surface of the water with its little trunk, swimming with its large webbed hind-feet and steering with the tail; just as *Trogontherium* will have done.

Rare indeed were the Carnivora, elephant, pig, ox, porcupine and monkey. During the almost 40 years that the Tegelen fossils have enjoyed scientific interest, not more than 1–5 finds of each species of all these animals are known.

In a damp, temperate climate this faunal assemblage lived in the marshy woods and bushes, and on the meadows between the slowly flowing meandrine river-branches of the vast delta. Judging from the manner in which both rhinos of Tegelen carried their heads, viz. much like *Diceros bicornis*, the black *Rhinoceros* of Africa (ZEUNER, 1936), it is clear that they fed on leaves of the brushwood as well as on the grass of the meadows, as did the deer also. The browsing of twigs is proved by the presence of remains of *Tilia* in the valleys of their molars.

It might have happened that an animal, when drinking, slipped from the slithery bank, or was caught in a flood, when at least once a year the river inundated the greater portion of the low delta, or became isolated by a stream-diverting, and perished. The swollen cadavers, sometimes transported by the river for a short distance or held where the animal died, fall apart by putrefaction, and so the bones were deposited at favourable places in the stream or in the staying waters. They are, just as the teeth, so perfectly preserved, with no trace of transport or of corrosion, that there can be no doubt, but that they lie still at the same place where they were imbedded. This may be proved further by the presence of rootless teeth in their alveoles. As soon as the soft, bluish grey clay is washed off the fossil jaws, the teeth fall out of their sockets.

The finds of fossils in the clay consist in isolated skulls, mandibles, teeth and bones. A more or less complete skeleton never has been met with, at best an extremity or a portion of a vertebral column. Quite undamaged specimens are rare in the collections, as in the clay they are wet and often so soft, that they become injured by the spade of the workmen; they break still more when pulled out of the clay. Moreover, when dried, they are often so burst, that they must be glued immediately on the spot, or the loss of some fragments would make a restoration impossible. It is an added difficulty that before the specimens are glued the attached clay must be washed off.

Although mechanical digging is being more and more used in the clay-pits of the brick-works in Tegelen, fortunately, there are still a few concerns, among others "Canoy-Herfkens", "Gebr. Teeuwen" and "Russel", where the clay is dug off with the spade, so that attention can be paid to any fossils coming to light. Notwithstanding the fact that the clay-layers worked during recent years are much poorer than those dug off about 35 years ago, when DUBOIS, KRAUSE and WEINGÄRTNER brought together the rich collections now preserved in Haarlem (Teylers Museum), Berlin (Preuss. geol. Anst.) and in Amsterdam (Zoolog. Museum of the Univ.), we owe it to the spade-digging by the firm of "Canoy-Herfkens" that in the last decennium new mammals, such as *Desmana tegelensis*, *Hypolagus brachygnatus* and *Pannonictis pliocaenica* have been recorded (SCHREUDER 1935–'43).

Moreover, of some mammals of which a few remains were already gathered in Tegelen, some important new documents could be saved, which will be described and figured in the present paper.

Naturally remains of large animals have the greatest chance of being found, it is therefore striking that bones and teeth of the ox are so scarce in Tegelen, much more so than remains of *Cervus*, *Equus* and *Rhinoceros*, leaving *Trogontherium* out of consideration. Oxen must have been a rare element in the Tegelen fauna, and this holds good for the elephant also, of which in the years of scientific interest in the deposits fragments of not more than three molars and of three determinable bones could be gathered. The bones of the elephant, when wet, are so little resistant that the spade cleaves them without the workman observing this.

That the clay-layers now in working are much poorer in fossils than those of former years is due to the fact that the fossils are heaped up in a certain region of the deposit, from which the working has shifted more and more. The proprietors expect that within ten years the rich spots will come into working again, and it is to be hoped that then there will be some scientific authority to prevent the destruction of the majority of these highly valuable fossils, which most of them have undergone during the clay digging of the past years.

Leptobos cf. *elatus* (Pomel)

(Text-figures 2–7)

The ox being extremely scarce in Tegelen, it is not surprising that it was not before 1930 that I detected a vestige. It was a large fragment of a scapula of Bovine character in the collection WEINGÄRTNER, at present in the Zoological Museum, at Amsterdam. In the same year a student in geology, JOH. BÖHMERS, returning from a trip to Tegelen, handed me three upper molars of a Bovine, which he had obtained from a clay-digger. They were added to the collection BÖHMERS and VAN BEMMEL in the Museum mentioned above. Shortly afterwards I observed among many molars of the large deer of Tegelen in a collection of the Nat. Hist. Museum, at Maastricht, a lower molar fitting perfectly to the upper molars mentioned.

So the list of Tegelen mammals has been enriched with an ox, first mentioned by BERNSEN (1932) in his lecture before the Geol. Society in the Netherlands, under the name of *Bibos* cf. *etruscus* Falc., as the form of the scapula and the size of the teeth and their fairly slight degree of hypsodonty, together with the occurrence in the Villafranchian Tegelen fauna, made it practically certain that we had to do with the much discussed slender ox with hornless females, known in Europe from Val d'Arno, Auvergne (Perrier, Senèze) and La Bresse (Chagny), localities which all have so many mammals in common with Tegelen. I am deeply indebted to the late Professor STEHLIN, who kindly compared the specimens from Tegelen with the material in the Natural History Museum at Basle, and moreover presented me with an upper and a lower molar of *Leptobos* from Val d'Arno, in order that I might convince myself by personal study of their great resemblance.

Regarding the scapula Professor STEHLIN wrote me: "Die Skapula passt gut zu solchen des *Bos etruscus* aus Val d'Arno,

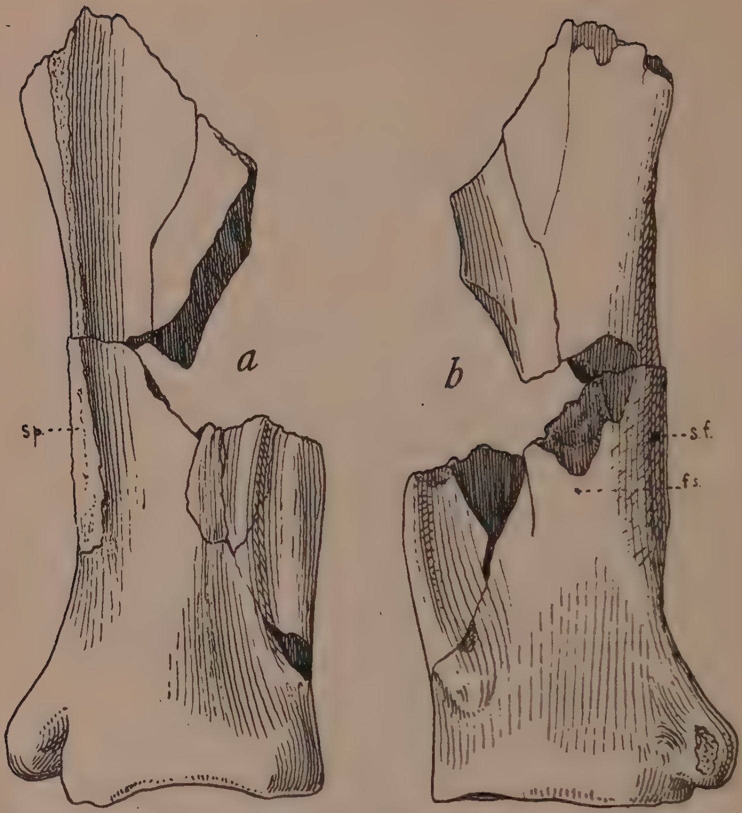

Fig. 2. *Leptobos* cf. *elatus*, Tegelen. Scapula sin., ½ × ; *a* outer side (spine broken off along the base), *b* inner surface. sp. base of spine; sf. supraspinal fossa; fs. facies subscapularis.

insbesondere auch in Bezug auf die Fossa supraspinata". The scapula from Tegelen (fig. 2) is badly damaged. The dorsal portion of the blade and the whole spine have been broken off. The glenoid cavity is broadly oval. Its rim, near the tuber, has crumbled away. Of the coracoid process only the place where it has been broken off can be seen. The largest diameter of the articular end (the tuber included) is 85 mm; perpendicular to it the diameter is 61 mm. (In the other large ruminant of Tegelen (*Eucladoceros tegulensis* (Dubois)) these measurements are 68 and 48.5 mm respectively). A characteristic feature is the slenderness of the bone and the bluntness of the edge between the facies subscapularis and the supraspinal fossa. The latter is quite flat (fig. 2*b*) up to 170 mm above the rim of the glenoid cavity. This feature is typical of *Leptobos*, as it is just the similarity of the supraspinal fossa in the specimen from Tegelen with those from Val d'Arno Professor S. mentioned in his letter.

The three upper molars from the Tegelen Clay are m^2 and m^3 sin., and m^2 dext., and belong certainly to the same dentition. Cement fills up the grooves and folds in places, but does not

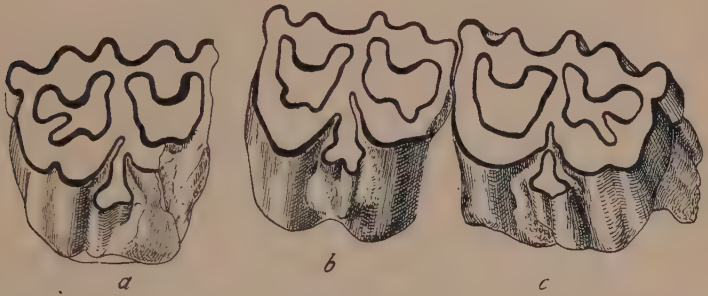

Fig. 3. *Leptobos* cf. *elatus*, Tegelen; upper molars, nat. size; *a* m^2 dext., *b* m^2 sin., *c* m^3 sin.

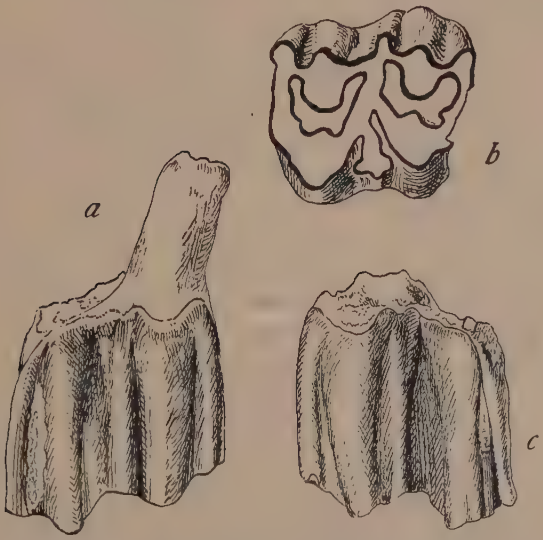

Fig. 4. *Leptobos* cf. *elatus*, Tegelen; upper molars, nat. size; *a* m^3 sin., outer side, *b* m^2 sin. crown-view, *c* m^2 dext., outer side.

cover the ribs, nor the sides of the crown. The enamel is rather thin and but slightly rugose.

In his excellent Monograph of the Bovidae of India PILGRIM (1939*a*) gives the following characters of the teeth of the genus *Leptobos*: "rather smooth enamel; upper molars rather elongate, outer lobes much compressed antero-posteriorly, folds and median ribs strong, prominent basal pillars."

The basal inner pillar of the upper molars shows a longitudinal ridge accompanied by a groove at each side; its cross-section widens on the inner side. A much less distinct pillar occurs on the outer side of the right m^2 at the base of the infold between the anterior and the posterior lobe (fig. 4*c*). It soon unites with the median rib. A similar faint pillar exists also at the corresponding place of m^3 (fig. 4*a*). On the inner side of the third lower molar (fig. 6*b*) a short basal pillar (DEPÉRET's "tubercule conique") is very distinct in the infold between the two lobes present. (The third lobe has got lost.)

The remarkable elongation of the Tegelen molars is apparent from a comparison with the measurements given by PILGRIM (p. 308) of the third upper molars in two skulls of *Leptobos falconeri* Rütimeyer from the Siwalik Hills, and with a specimen of m^3 of *Leptobos etruscus* Falc. from Val d'Arno.

	L. falconeri		*L. etruscus*	*L. elatus*
m^3	♀ Br.Mus 48037	♂ Br.Mus 40887	Val d'A.	Tegelen
1. ant.-post. diam. at middle of crown	31	32.5	31.5	29
2. transverse diam. at base	27	28.5	28.5	24
1 : 2	115	114	111	121

Measurements of m^2 I found nowhere in literature. In both specimens from Tegelen they are:

m^2	dext.	sin.
ant.-post. diam. at middle of crown	28.4	26.6
transverse diam. at base	25.5	25.5

The resemblance to m^2 of *Leptobos elatus* from Chagny, figured by DEPÉRET (in DELAFOND et DEPÉRET, 1893, Pl. XIII, fig. 3) is striking. Moreover, the short pillar in the middle of the outer

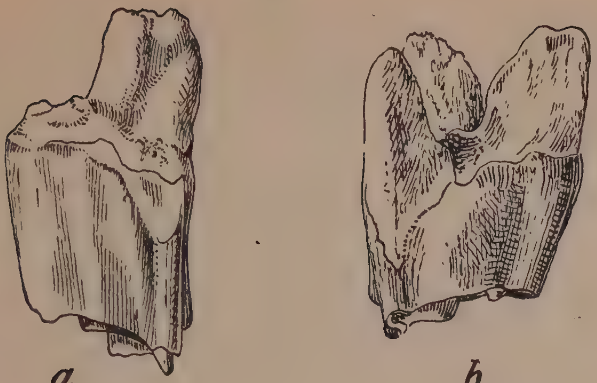

Fig. 5. Third upper molars, ant. side, nat. size; *a* m³ sin. of *Leptobos* cf. *elatus*, Tegelen; *b* m³ dext. of *Leptobos etruscus* from Val d'Arno.

side is quite identical with that on the inner side of the lower molar from Tegelen (fig. 6*b*). Measured on the figure by DEPÉRET the ant.-post. diam. at the middle of the crown is 27.8 mm.

The last upper molar from Tegelen is less brachydont than the one from Val d'Arno (fig. 5*b*) I have at hand.

DEPÉRET (1884, p. 275) gave the following description of the dentitions in the rich collection of *Bos elatus* Pomel (ex Croizet MS.) from Perrier in the Paris Museum: "Comparées à celles des Boeufs actuels, les molaires supérieures, de forme carrée, présentent à la jonction de la couronne et de la racine un collet apparent qui manque à ces derniers; l'émail est plus mince, et le cément moins développé ou presque absent. Les colonnettes interlobaires sont plus étroites, et moins solidement accolées au fût" And later (in DELAFOND et DEPÉRET, 1893): "Nous avons décrit en 1884 les caractères de ce Bovide pliocène. Nous n'avons observés dans l'horizon de Chagny que deux arrière-molaires supérieures (fig. 3 et 4) où l'on retrouve tous les caractères du *B. elatus* d'Auvergne." These two molars are preserved in the collection of the Ecole des Mines, Paris.

When we compare WÜST's figures of his *Leptobos*? from Süssenborn with the molars from Tegelen and with the figure of the molar from Chagny, the difference is so apparant (the latter are so much more brachydont and smaller, the enamel is thinner, the form of the median accessory pillars is different, etc.) that it is precluded that this Bovide can be a *Leptobos*. Moreover, its occurrence in the Süssenborn gravels, deposits which are nowadays placed into the Mindel-glacial by German authors (HELLER, 1938) makes it highly improbable that so typical a Villafranchian Bovine as *Leptobos* can come into consideration here.

Respecting the lower molars of *Bos elatus* Pomel DEPÉRET wrote (1884, p. 275): "Les molaires inférieures sont plus étroites et plus allongées; elles ont un aspect antilopin qui frappe à première vue, bien qu'on y retrouve les principaux caractères des Boeufs, et notamment la forte saillie de la côte médiane à chacque lobe des arrière-molaires. Toutes sont pourvues d'un collet, moins marqué pourtant que dans les Cerfs. Les arrière-molaires portent en avant un gros pli transverse d'émail, comme celui des Chèvres, ...". This fold is very distinct on the m_3 from Tegelen (fig. 6).

It seems that the "Bovine lower molar", figured by NEWTON (1891, Pl. III, fig. 1) from the Red Crag Nodule-bed of Boyton is the size of a lower molar of *Leptobos elatus*. It would be of interest to compare it, and "similar teeth" mentioned by NEWTON (p. 21) from the Red Crag, with lower molars from the French localities. DEPÉRET's words: "Quant aux Bovidés de l'horizon de Saint-Prest et du Forest Bed ils paraissent se rapprocher tout à fait, comme l'espèce de Saint-Cosme, des types quaternaires" are in complete accordance with those of PILGRIM (1939*b*): "*Leptobos* is the only Bovine definitely known from the Villafranchian of Europe. It is replaced in the Cromerian by *Bos* and *Bison* of a rather modern type."

Besides the scapula and the teeth mentioned, two other

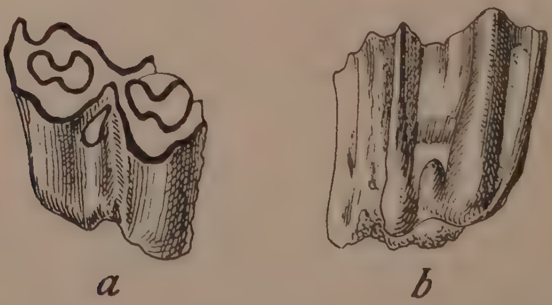

Fig. 6. *Leptobos* cf. *elatus*, Tegelen. M_3 sin. (lacking hind-lobe); nat. size. *a* crownview *b* inner side.

specimens of Bovine character have been met with in Tegelen, viz. the middle portion of a humeral shaft (coll. Böhmers en van Bemmel, Zool. Mus., Amsterdam) and a fragment of a horn core (Nat. Hist. Mus., Maastricht). During the forty years that the Tegelen fossils have met with scientific interest no other member of this family, could be recognized, and thus we will refer the remains in question provisionally to *Leptobos elatus*, the more so as the ratio of the measurements of the humerus to that of the large deer of Tegelen is the same (6 : 5) as that which exists between the measurements of the scapula in both these ruminants.

The humeral shaft shows the minimal width to be 41 mm, and the ant.-post. diam. at that place 50 mm. In the large deer from Tegelen, the strongest humerus I saw has a minimal width of 34.4 mm. Thus the fragment of shaft is too strong to belong to that deer, but for an ox it is remarkable slender, which is due to the slender build of *Leptobos*, as may be demonstrated by the following measurements of metacarpals, borrowed mainly from Pilgrim (1939, p. 204):

metacarpals	*C. tegul.*	*Taurotr. oryx.*	*Lept. ei.*	*Bos primig.* Freudenberg, 1914, p. 99	*Bison bison* Brit. Mus.	Dutch domestic cow
1 length	273	313	240	246	209	223
2 width, middle	27–29	34	35	56	43	36
3 width, prox.	48–54	63	58	95	69	72
4 width, distal	46–49	62	55	88	75	68
$\frac{100 \times 4}{1}$	17–18	20	23	36	36	30

Thus the width of the bone of *Leptobos* nearly approaches the eland, but the length is less, although still greater than in the Bison. The proportions betray more likeness to the robust Antelopes than to the Bovines.

The horn core represents merely the distal extremity, as it is broken off at the thicker end. The object at hand has a length of 21 cm; max. and min. diameter of the cross-section are 49 and 45 mm respectively. It is subcylindrical, with a well-marked flattening. The centre of the core is occupied by four wide longitudinal channels, separated from each other by two partitions forming an irregular cross. These channels end at a distance of 13 or 14 cm from the top, the utmost point of which appears to

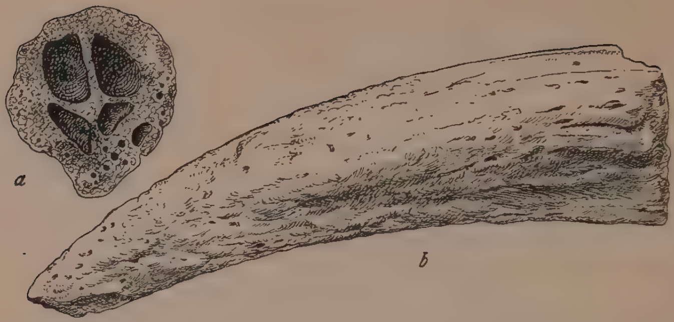

Fig. 7. *Leptobos* cf. *elatus*, Tegelen. Fragment of horn-core, ½ nat. size; *a* cross-section, *b* side view.

have been broken off obliquely. The outer surface is coarsely ribbed, with a slight indication of a twist. Probably the single distinct keel, along the weakest curve of the object, is the inner one, which, according to PILGRIM (1939*a*, p. 305), is well-marked in *Leptobos elatus*.

RÜTIMEYER (1867) gave good figures of the horn-cores of *Leptobos etruscus* in Pl. I, figs. 3–5 and in text-fig. 9; moreover, in 1878, on Pl. VII, fig. 3. There are no figures of horn-cores of *Leptobos elatus*, as far as I know, but they do not differ materially from those of the Italian form. In *L. elatus* the horns diverge at an angle of 130° (in *L. etruscus* of 120°), and in both they stand upon a kind of socles formed by the frontals. At their base they are directed backwards and outwards, then make "eine sehr elegante Curve" upwards and forewards. The distal end bends somewhat backwards again. In the skull of the Museum at Florence the length of the core is 52 cm. This size approaches that of *Bibos banteng*; the general form of the horn resembles that of *Bos primigenius*, the basal portion excepted which is also directed outwards, but not so much backwards in the latter.

The remains of *Leptobos* are abundant in the Upper Arno Valley. In Senèze the species was much less common. Also the remains from Perrier and from Chagny prove that *Leptobos* did not occupy a prominent place in the French Villafranchian faunas. In Tegelen it must even have been rare.

The recent, splendid Monograph of PILGRIM (1939*a*) releases me from giving any remarks about the phylogeny of the genus and its much discussed place between antelopes and oxen.

Leptobos ranged from Java to Western Europe, and died out there before the end of the Günzian period. Probably its last representatives lived in the Günz-interstadial (Tegelian).

Archidiskodon meridionalis (Nesti), archaic form

(Plate III, fig. 2 and text-figs. 8–10)

At the time of DUBOIS' investigation of the Tegelen Clay no remains of *Elephas* had been gathered yet (DUBOIS, 1904, 1905*b*). It was the Reverend RICHARZ (1921) who first mentioned the elephant as an indutable component of the Tegelen fauna, when he had observed a fragment of a molar in the collections of the Mission-House at Steyl, near Tegelen. For confirmation he sent it to MAX. SCHLOSSER, who referred it to *El. meridionalis* Nesti. The Rev. RICHARZ who had come to the same conclusion, merely mentioned the find, but gave neither description nor figure. This was done by BERNSEN (1930), after having compared the fragment with several specimens in the British Museum. In the same paper BERNSEN described and figured a fragment of a second or third molar of the same species from Tegelen, which is preserved in the Nat. Hist. Museum at Maastricht.

RUTTEN (1909, p. 16) had already recorded a mandibular condyle of *Elephas* with the following words: "Vielleicht muss zu *El. meridionalis* ein Condylus mandibulae gestellt werden, der in Jammerdael bei Venlo gefunden wurde und an dem noch der fette graue Ton von Tegelen haftet." There can be little doubt about the belonging of this specimen to *Arch. meridionalis*, the elephant of Tegelen, as the molar fragment recorded by RICHARZ was found at the same place, viz. the claypit of "Canoy, Herfkens & Co. in der Jammerdaalschen Heide, Tegelen."

The remains of *Archidiskodon* thus being very scanty, I was pleased when JOH. BÖHMERS handed me some years ago a molar of an elephant, which he obtained from a clay-digger in Tegelen. It is now preserved in the collection BÖHMERS and VAN BEMMEL, in the Zoological Museum of the University at Amsterdam.

This largest tooth-fragment known of the Tegelen elephant consists of 4 ridges, and the posterior talon. The roots have been broken off. The talon and the two hindermost ridges are undamaged, the two ridges in front of them are damaged in such a way that, at the outer side of the crown, the dentine in the centre of the ridges is entire, but the enamel layer surrounding

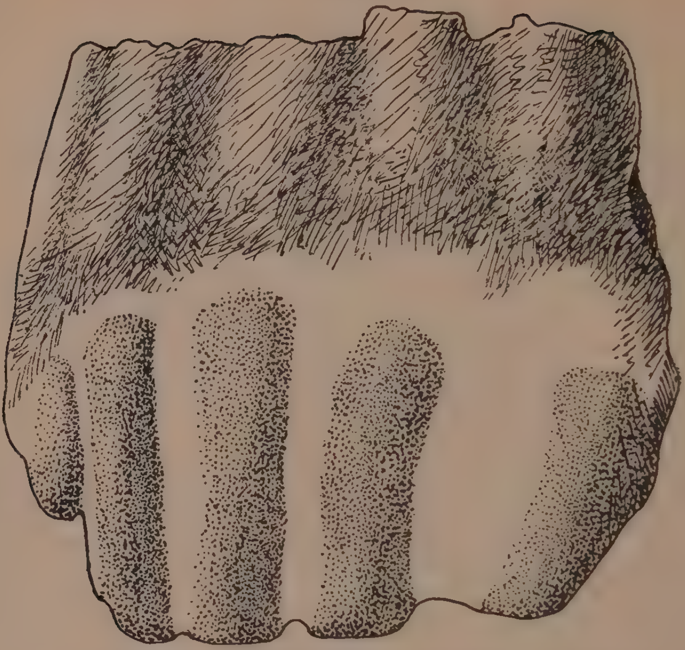

Fig. 8. *Archidiskodon meridionalis,* Tegelen. Posterior half of D^4 sin., int. side; nat. size. (Enamel is spotted; cement is white).

it has been broken off at the extremity of the ridges. Still another ridge is represented, but merely by some fragments. The enamel layer, measured at the broken places, appears to vary in width between 4 and 4.5 mm; the ant.-post. diam. of a ridge is 14 mm. On the crown-surface the four ridges together occupy as much as 62 mm of the length of the tooth.

The low laminar frequency and the considerable thickness of the enamel afford the irrefutable proof that also this tooth must be referred to *Archidiskodon meridionalis*, like the other two. When, however, we compare the measurements given by Bernsen of the hindmost ridge and the posterior talon with those of the new tooth, it is obvious that the latter is a milk-molar. The fragment quickly increases in width from behind forewards. The talon ends 20 mm beneath the wearing-surface of the tooth, and was hidden in the dense coat of cement covering the tooth on the posterior end. On the sides the cement is absent at the ridges, so that their max. width mentioned in the table also holds good for the whole crown at those places. The talon ends into three

	Width				Height		
	D⁴			M² or M³	D⁴		M² or M³
	Tegelen	Italy	Forest-Bed	Tegelen	Tegelen	Italy	Tegelen
post.talon	17			± 60	22		—
7th ridge	41			90–92	45	45,63	± 100
6th ridge	54	50			45		
5th ridge	65		44,35		40		
4th ridge	65	60			35	60	
3rd ridge	?				30		

digitations; the talon of the true molar (M² or M³) described by Bernsen is damaged, but must have had as many as seven digitations.

Whereas descriptions of true molars are abundant in literature, those of milk-molars are rather scarce. In their Monograph on Pliocene elephants, Depéret et Mayet (1923, p. 135) leave out of consideration "toute description des dents de lait et même des deux premières arrière-molaires". It was from the other valuable publication on *Arch. meridionalis* (Weithofer, 1890) that the rank of the new Tegelen tooth in the dentition could be established, as being the last milk-molar (D_1 of Weithofer, D_4 of Zittel, ml³ of Depéret, Mayet and Roman, M³ of Pavlow, MMIII of Leith Adams, DIII of other authors).

As the tooth is merely a fragment, it is the width and the height of a fixed ridge, which must guide us in determining the place of the tooth in the dentition. A slight convexity of the wearing-surface, in longitudinal as well as in transverse direction, indicates that the fragment is that of an upper tooth, and a slight curve backwards, especially of the posterior enamel figures on the crown-surface, also points to this. The rather straight side of the crown surface will then be the lingual side, and the more convex side the labial one, and thus the tooth is a left upper one, D⁴ sin.

The laminar formula of D⁴ in *Arch. meridionalis* ("formes type du Val d'Arno") is t. 7 t. Thus, in the Tegelen tooth-fragment the anterior talon and the two foremost ridges (first and second) have got lost. Ridge 3 is represented by some sherds. The ridges 4–7 and the posterior talon are well preserved in situ.

The tripartition of the enamel figures at the wearing-surface is distinct, and best seen at the scarcely worn ridges 6 and 7. The talon ending so far beneath the crown-surface naturally does not show any trace of wear. The figure of ridge 7 displays the cross-section of four digitations, the two median being smaller than that on either side. In the figure of ridge 6 the two median digitations have fused, and a small one separates them from a large labial digitation. In the enamel figure of ridge 5 only one, the lingual, digitation is still independent; the others have fused to one broad laminar figure with two constrictions indicating digitations. Ridge 4 displays only one broad laminar figure, and as far as can be deduced from the fragments present, the figure of ridge 3 was quite the same.

WEITHOFER saw merely three specimens of D^4 in the Florence Museum, of which a pair are in situ. The other tooth was already described by FALCONER. WEITHOFER (1890) figured it on his Pl. VIII, fig. 1. Of the pair the right one shows a width of 50 mm at ridge 6 and the left one a height of 63 mm at ridge 7. The Tegelen tooth thus is about as broad, but considerably lower, viz. 45 mm at ridge 7. The figured Italian specimen, however, is quite as high as the Tegelen tooth at ridge 7, but it is distinctly narrower, as can be measured at the enamel figures of ridges 4–6 on the Plate. The great width mentioned by WEITHOFER is caused by the very thick coat of cement, which, as contrasted with the Tegelen tooth, covers the sides of the tooth, especially at the posterior half. The enamel figures are considerably broader in the Tegelen tooth. Another D^4 of *Arch. meridionalis*, in the Museum of Montevarchi, shows at ridge 4 the height as well as the width to be 60 mm. The Tegelen tooth is much lower there, perhaps partly caused by a more advanced wear.

Neither SOERGEL (1912) nor PAVLOW (1910) mention any milk-molar of *Arch. meridionalis*. LEITH ADAMS (1881) did, but no height-measurements of the teeth are given.

These are an upper "ultimate Milk-Molar" (No. 9 of the Norwich coll.) from the Forest-Bed, Bacton, and a dito (King coll. Jermynstreet Mus., No. 92) from the Forest-Bed, Cromer. The (probably max.) width of these English teeth is 44.5 and 35.5 mm respectively, thus much narrower than the Italian and the Tegelen specimens of D^4. The Tegelen tooth combines the greatest width with the smallest height mentioned in literature for D^4 of *Arch. meridionalis*, which justifies the addition: archaic form.

Lately ZONNEVELD (1942) mentioned a D^4 of *Arch. meridionalis* from Tegelen (Geol. Mus. Leiden, St. 32266). It will have been acquired by the Museum after the study of BERNSEN was published (1930). The specimen in question (fig. 9) is a fragment of which only one ridge is complete. Of the following ridge no more than a portion of the anterior enamel layer is still existent, and that at the left side. The ridge preceding the entire one shows a complete posterior wall, but the anterior wall has crumbled away by wear down to the base of the root. This renders it probable that the fragment is a stump, pushed out by the first true molar.

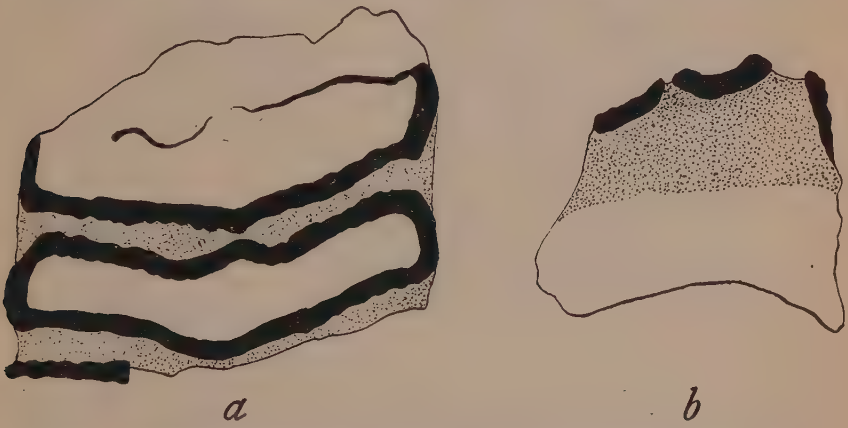

Fig. 9. *Archidiskodon meridionalis,* Tegelen. Fragment of D_4; Leiden Geol. Mus. St. 32266. nat. size. *a* crown view, *b* side view. (Cement is spotted; dentine is white; enamel is black).

The height of the enamel ridges preserved is nowhere more than 21 mm. The width of the entire ridge is 56 mm, the preceding one is 52 mm broad, that following the complete one is 57 mm. The thickness of the enamel varies between 3 and 4 mm, the ant.-post. diam. of the entire ridge is 12–14 mm. It shows a dilatation in the median line, whereby it almost touches the adjacent ridges. The fragment shows the base of both roots (fig. 9*b*).

The size points to a last premolar, and the slight transverse concavity of the wearing-surface, together with a weak anterior concavity of the enamel figures to an inferior one.

The width agrees with that measured by WEITHOFER on some Italian specimens, in one of which the max. width is ± 60 mm, in another 55 mm. In 5 specimens the max. width varies between 45 and 60 mm.

A large fragment of a molar of an elephant, fished out of the Scheldt-mouths and preserved in the Leiden Geol. Mus. (St. 40094), is represented by six ridges of which two are hardly worn, and the other unworn (fig. 10*a*). The enamel pattern has come to light through the polishing away of the top of the two hindmost ridges. The roots are missing, so that at the base of the crown the lower ends of the enamel folds protrude freely, as the dentine, otherwise filling the spaces between them, has partly fallen out. In this way the fragment has broken into three thick discs, the fractions running through the spaces between the bases of the enamel folds and higher up just transversely through the middle of the enamel figures. Our figure 10*b* gives a look at the surface caused by the fracture through the third ridge (which has not yet been touched by wear). The max. width of the fragment is 85 mm, the height 105 mm. Probably the tooth is a left lower second molar or a right upper one. The colour of the enamel, the thickness of which varies between 3 and 4 mm is bluish grey, that of the dentine and the cement is walnut-brown, colours typical of fossil Tegelen teeth. The pattern exposed by polishing exists in a row of some annular figures. Our fig. 10*b* displays at the top the same situation, but it shows that in successive stages of wear some median annular figures will be flanked by a pair of lateral laminar figures. Then their will be

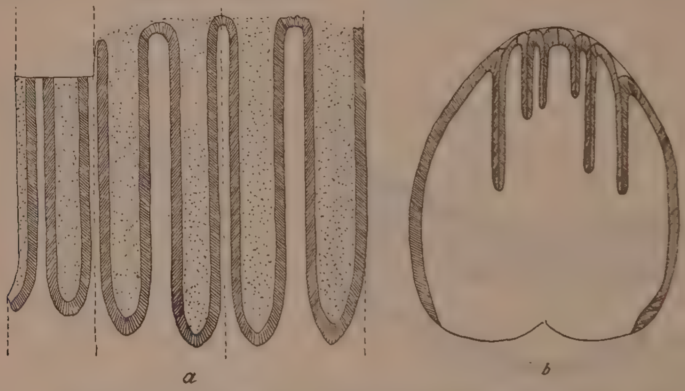

Fig. 10. *Archidiskodon meridionalis*, Scheldt-mouths. M_2? (Leiden Mus. St. 40094), $^2/_5$ nat. size. *a* section near to the median plane (somewhat schematic), *b* seen on a fracture-surface. Cement is spotted, enamel is hatched, dentine is white, ----- fractures.

three laminar figures and finally there will be one very broad laminar figure occupying the whole width of the crown. The laminar frequency of this molar is 4½. All characters point to *Archidiskodon meridionalis*, archaic form, the elephant of the Tegelen horizon which, as Dr. J. F. Steenhuis kindly informed me, besides in Limburg and Noord-Brabant, is present also in the underground of the province of Zealand, east and north of a line which can be drawn (from the south-east to the north-west) through the Wester-Scheldt, the isle of Zuid-Beveland, probably through Noord-Beveland, and further between Walcheren and Schouwen. The label belonging to the object indicates a vague locality, namely: "Zeeuwsche wateren".

Rutten (1909) recorded six first molars and some bones of the South-elephant, found in a clay-pit at Oosterhout (Noord-Brabant). These molars are astonishingly broad for first molars of the species.

On the fragment of the Tegelen tooth (m^2 or m^3) described by Bernsen the laminar frequency is 4½. This, together with its lowness, and the considerable thickness of the enamel layer, again proves the truth of Bernsen's statement, namely, that the elephant of Tegelen belongs to the archaic form of *Arch. meridionalis* (Mayet et Roman, 1923, p. 14 and Depéret et Mayet, 1923, p. 136, etc.), just as the elephant of Val d'Arno, and that of Senèze and of Chagny. (Stehlin (1923, p. 274) does not accept the name of *Elephas planifrons* Falc. given by Depéret et Mayet to the form of both the latter localities.)

Pohlig, in 1888, gave the generic name of *Archidiskodon* to the Southern-elephant and this name has been upheld by Osborn (1918–1935) as well as by Schlesinger (1912) and by Hopwood (1935), thus we have termed the brachyodont, laticoronate, parsilamellate, pachyganal elephant of Tegelen *Archidiskodon meridionalis* (Nesti), with the addition: archaic form.

Together with the upper milk-molar described above several fragments of skeleton-bones have been gathered, among which merely the corpus of a dorsal vertebra could be recognized. It is badly damaged, but the anterior surface and part of the posterior are complete, as is also an articular surface for a rib. The antero-posterior diameter of the corpus is 7 cm approximately.

The common opinion of the German palaeontologists is 1° that *Arch. meridionalis* is a descendant of *Arch. planifrons* (Falc.) of India and of the Lower-Villafranchian of Europe. However, the identity of the Asiatic and the European form is not yet irrefutably established (DEPÉRET et MAYET, 1923, p. 123), and 2° that *Elephas primigenius* has descended from *Arch. meridionalis*, by the intermediacy of *Elephas trogontherii*. OSBORN (1925) agrees with this point of view as regards the descendence of *Arch. meridionalis*, but as to its offspring his hypotheses are that the "giant Southern Mammoth of the Pliocene and Lower Pleistocene forests of Italy, France, (Holland, A. S.) and the British isles, adapted to shrub-browsing and to the crushing of great masses of leaves and twigs, wandered from there to America in Upper-Pliocene and Pleistocene time where this majestic animal was discovered in Nebrasca and described by LEIDY (1858 fide OSBORN) as ELEPHAS IMPERATOR. The phylum apparently becomes extinct in Lower Pleistocene time, both in Europe and in America."

About *Elephas trogontherii*, termed *Parelephas trogontherioides*, the North Temperate Mammoth, OSBORN wrote: "It has taken many years to disentangle the lineage of this great immigrant from that of the Southern Mammoths on the one hand and that of the Woolly Mammoths on the other". According to OSBORN, it is now a well established fact that the Jeffersonian Mammoth (an American species, therefore, and not the European *Mammonteus primigenius*) came from *Parelephas*, smaller and more primitive ancestors which wandered in the north temperate forests and meadows of western Europe during the first half of the Age of Man. "These European forebears replaced *Arch. meridionalis* and were in turn replaced by great herds of the Woolly Mammoth, adapted to feed upon the hard grasses of the northern steppes and tundras, that entered Europe in the later period of the Age of Man. Whereas the European branch of *Parelephas* became extinct, the American branch flourished exceedingly.

DEPÉRET et MAYET (1923) agree with OSBORN in denying any phylogynetic contact between *Archidiskodon meridionalis*, *Parelephas trogontherii* and the mammoth.

BELIAJEVA (1936) gave a map of the distribution of *Arch. meridionalis* (Nesti) in Europe. If the Dutch localities in Zealand (Scheldt-mouths), in Brabant (Oosterhout) and in Limburg (Tegelen) had been put in, they would have filled up the gap between the English and the German localities.

Macaca florentina (Cocchi)

(Text-figures 11–13)

Only once has a monkey been recorded from Tegelen, and that by Bernsen (1930, 1931), who described and figured the lower jaw of an old male with all the teeth, except the incisors, the canine, and the anterior premolar of the left side. This jaw lacks the ascending rami and is imbedded in a concretion of clay-iron-stone. Bernsen discovered it in the collection of the Mission Museum at Steyl, near Tegelen.

The dentition is so much worn off that merely the bases of the crowns are preserved. Notwithstanding this, by a thorough comparison of the horizontal ramus and the measurements of the teeth with many jaws of recent monkeys, Bernsen was able to conclude that the Tegelen monkey is a *Macaca*, bearing a great resemblance to *Macaca florentina* (Cocchi) from Val d'Arno; hence he termed it *Macacus* cf. *florentinus* Cocchi.

Shortly after this six isolated lower teeth of a monkey were gathered in the Tegelen Clay (Clay-pit "Russel-Tiglia"), belonging to one and the same young dentition. They are i_1, p_4, m_1 and m_2, all of the left side, and m_1 and m_3 of the right. In contrast to the old dentition mentioned above, these young teeth are perfectly preserved and hardly worn. The m_3 is a germ lacking the anterior pair of cusps, but showing to the perfection the much discussed hind-lobe. These teeth are part of the Tegelen collection Böhmers and van Bemmel, in the Zoological Museum of the University of Amsterdam.

Quite the same perfect state of conservation is displayed by some isolated upper teeth found a few years afterwards in Tegelen, and now preserved in the Natural History Museum, at Maastricht. These are i^2, c, p^3 and p^4, all of the left side. They belong to the dentition of an adult male.

Thus we are able now to compare the well-preserved teeth from Tegelen with those of *Macaca florentina* from Val d'Arno, which have been accurately described and figured by Cocchi and Ristori.

The Italian remains are of the lower jaw:

1. the type of *Aulaxinuus florentinus* Cocchi (1872, Pl. I, figs 3–5), which is a lower jaw with the dentition of a male;
2. left mandibular ramus with p_4–m_3, demonstrated by Forsyth Major, 9 March 1879, at the meeting of the Società Toscana di Scienze Naturali,

in Pisa (cf. Proc. verb. p. LXXII), and figured by RISTORI (Pl. VIII, fig. 30);

3. lower jaw with dentition (left ramus and ant. half of the right) of old female (RISTORI, Pl. VIII, figs. 35 and 36).
4. isolated m_2 and m_3 (RISTORI, Pl. VIII, figs. 31–34) and i_2 (ibid., figs. 20 and 21);
5. isolated p_4, m_1, m_2 and m_3 from Mugello, which are the type-specimens of *Macacus ausonius* F. Major [1]) (RISTORI p. 232 and p. 237, Pl. VIII, figs. 22–29);
6. damaged lower jaw recorded by PORTIS (1916) (non vidi; fide FREUDENBERG, p. 131, foot-note);
7. some isolated teeth (LAWLEY: Scimmie fossili d'Orsiano (Soc. tosc. Sci. nat. 1879, proc. verb. p. LXXVII)).

Thus the lower jaw and dentition are fairly well represented, but of the upper has been preserved only:

1. a maxillary fragment with m^1–m^3 in situ and some alveoles of the premolars (FORSYTH MAJOR, 1872, p. 89 and RISTORI, p. 226, last paragraph);
2. isolated m^2 (RISTORI, Pl. VIII, figs. 17–19).

As to the posterior lower premolar (p_4) in the type jaw, COCCHI mentioned two sharp cusps on the anterior half of the crown, standing opposite to each other and united by a transversal bridge. In the tooth from Tegelen these cusps are well-developed and hardly worn; the anterior is the larger of the two, and three-sided pyramidal, the exterior more compressed from side to side and somewhat lower. The transversal crest is crossed by a longitudinal groove fading out from the crest backwards and deepening from the crest forwards, where it ends in the anterior shelf at the base of the anterior margin of the tooth. The posterior half of this premolar is occupied by a cup-shaped heel, nearly as broad as the anterior portion of the crown, and surrounded by a faintly crenulated rim which is equally high all round. This situation is well seen in Ristori's figs. 22 and 23 on Pl. VIII. The Tegelen tooth had two roots, which have got lost.

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[1]) RISTORI, p. 236: "Su questi denti il F.-MAJOR aveva fondato la sua specie *Macacus ausonius*" and p. 232: "il FORSYTH-MAJOR mi disse di avere fondata la sua nuova specie *Macacus ausonius*, che io fin da principio mi permisi di ritenere sinonima di *Inuus florentinus*." F. MAJOR promised (1872, p. 95) a detailed monograph on his *Macacus ausonius*, but parts of that species have been neither described nor figured by that author. In the publication of 1884 on the fauna of the Arno-Valley he gives some lists which demonstrate the progress in knowledge respecting that fauna. In the list of 1872 *Macacus florentinus* is the sole Primate mentioned. In that of 1874, besides "*Macacus florentinus* Cocchi sp.", a second monkey appeared, viz. "*Macacus ausonius* n.sp." As regards that list the author referred to his "Considerationi sulla Fauna dei Mammiferi, etc." of the same year, but the species in question are merely mentioned there, without any commentary. The only words of F. M. about *Mac. ausonius* that I could find are those at the end of the "memoria" of 1872 (meeting of 1 April 1872): "quelques dents isolées de la mâchoire inférieure, qu'un rapide examen m'a paru indiquer une espèce de *Macacus* qui pourrait bien être différente des deux pièces de Val d'Arno dont je viens de parler. Ces dents proviennent de Mugello dans le Val d'Arno."

The lower molars are of the common type in *Macaca*, increasing in size from the front backwards. The crowns of the first and the second molars are undamaged, but the roots have been broken off.

As a matter of course, the m_1 has suffered more from attrition than either of its neighbours. The outer cusps thus show an islet of dentine near their top, and the posterior shelf of the crown has become quite flat, because its rim, which forms the posterior margin of the tooth, has been worn away. Also the rim of the anterior shelf has vanished. Seen from the outer side, the outer cusps display a slight dint at each side of the cusp midway of the height. These dints indicate the limit between cusp and shelf. The dints isolate something like an outer median cusplet between the cusps, which, however, instead of a top shows a horizontal wearing-facet. The vertical groove separating this cusplet from the protoconid is deeper than that between the cusplet and the hypoconid. There is no trace of a cingulum on the tooth.

M_2 has been hardly worn. It is somewhat larger than m_1, but for the rest the two molars agree in form. The median outer cusplet is less distinct; it is merely indicated.

The first pair of cusps on the third molar (fig. 11) has got lost, but the second pair with the hind-lobe (heel, talonid or 5th cusp) is undamaged. This tooth has not yet erupted, and is merely a germ. The halfmoon-shaped heel consists of a higher portion which, seen from the outer side, forms the third outer cusp of the molar. The rest of the heel is lower, and separated

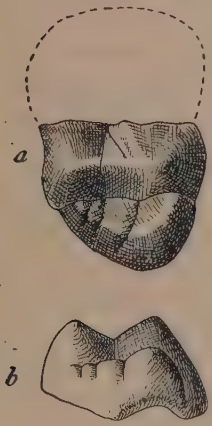


Fig. 11. *Macaca florentina*, Tegelen. M_3 dext. (posterior half); 3 ×. *a* crownview, *b* from behind.

from the higher portion by a fine vertical furrow, and is itself divided by two similar fine grooves into three small portions of equal height (fig. 11*b*), joining the endoconid.

In the description of the moderately worn dentition of the type-mandible, COCCHI wrote respecting m_3 that the heel is divided into two unequal parts by a shallow groove near to the inner side of the tooth, so that the larger portion of the heel lies at the outer side, the smaller at the inner (COCCHI, Tav. I*a*, figs. 3–5). He assumed this bipartition of the heel to be a feature which distinguishes the fossil last molar from that of recent *Mac. sylvana* (L.) (*Macacus* or *Inuus ecaudatus* Geoffroy), to which, on the whole, the dentition shows most resemblance, but where the heel of m_3 displays a tripartition. RISTORI had seen that in *Mac. sylvana* the heel may be divided into two or into three lobes. In the fossil specimens of m_3 he saw two grooves in the outer portion of the heel. It was merely in the young isolated m_3, belonging to the set of teeth on which, according to a verbal communication made to RISTORI, F. MAJOR founded his *Macacus ausonius* n.sp. (1874), that RISTORI saw two grooves "più evidente" on the inner portion of the heel. Thus, this young m_3 most resembles the unworn specimen from Tegelen. It is apparent from our figure that by continued wear these inner grooves will disappear, as they fade away at half the height of the wall. The figure demonstrates, moreover, that the more the tooth is worn off the more the outer portion of the heel will increase in size with respect to the inner, as the outer part is slightly conical.

ZDANSKY (1928), in his exemplary description of the m_3 dext. from Choukoutien (termed Cynopithecide gen. et spec. indet. by Z., and *Macacus robustus* by YOUNG (1934)), emphasizes the discutable value of the partition of the talonid in Cercopithecidae. This Chinese specimen differs from the Tegelen m_3 in the fact that the talonid consists of two cusps, one in the median line of the tooth, the other between the first-named and the endoconid; both talonid-cusps are separated by a faint groove. It appears from YOUNG's description that in his *Macacus robustus*, of which several lower and upper dentitions have been preserved, the talonid of m_3 may show an accessory cusplet.

Whereas the length of m_3 in the four Italian specimens mentioned above varies between 11,3 and 12.9 mm, and that of the new tooth from Tegelen cannot have been more than 11.7 mm, the length given by BERNSEN, viz. 15 mm, is rather astonishing.

I think the difference is mainly due to the fact that, in concretions of clay-ironstone, bones and teeth as a rule are intersected by numerous cracks. That this is also the case in the dentition described by BERNSEN is clearly shown by the photographic figures. Therefore the length of the molars must be diminished by the combined width of these cracks, and the length of the whole dentition by all the cracks plus the artificial spaces between the teeth, caused by the same extension.

The upper teeth (i^2, c, p^3, p^4) preserved from Tegelen are not represented in the Italian material of *Macaca florentina* (Cocchi), at least I have found them nowhere mentioned in literature. The upper teeth from Tegelen all show sharply defined, rather large wearing facets, and certainly belong to one and the same dentition of an adult male. They are all preserved with the roots.

The form of the incisor is that of all monkeys. The crown is less high than in the lower incisor; the root is less compressed from side to side, but shows a distinct curve backward. Together with the root the height of the tooth is 19.0 mm. The height of the crown is 8.2 mm, at the labial side, the max. width of the latter is 4.7 mm. At the base of the crown the ant.-post. diam. of the root is 5.0 mm, the width 3.6 mm.

The upper canine (fig. 12) is not stronger than that in strong males of *Macaca sylvana* (L.) and almost of the same form. This is in accordance with RISTORI's findings after a thorough comparison of the type (lower) jaw of COCCHI with that recent species, namely, the fossil lower canines are noticeably robust, but not different in form from those of *Mac. sylvana*. An equally deep and narrow groove runs along the anterior side and broadens out along the root.

The upper canine with the undamaged root is 54 mm long (rectilinear), of which the crown occupies 26.7 mm. The crown is scimitar-shaped; the width at its base is 7.2 mm, the ant.-post. diam. 11.2 mm.

In a strong male skull of *Macaca sylvana* (Mus. Nat. Hist., Leiden, cat. *a*), in which the molars are the same size as the Tegelen ones, I measured on the canine a crown-length of 25 mm, at the base of the crown 9 and 12.5 mm. Here, thus, the

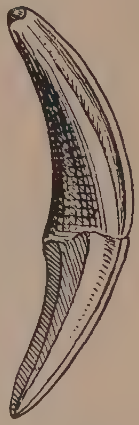


Fig. 12. *Macaca florentina*, Tegelen. Left upper canine, nat. size; lingual side.

Measurements of lower last premolar and molars in fossil *Macaca*

		Macaca florentina				*M. prisca*	*M. tolosana*	*M. robusta*		*M. sivalensis*
		Val d'Arno		Tegelen		Montpellier	Montsaunès	Choukoutien		Hasnot
		COCCHI 1872	RISTORI 1890		BERNSEN 1930	GERVAIS 1859	HARLÉ 1892	YOUNG 1934	ZDANSKY 1928	PILGRIM 1915
p_4	length	5	6.1–6.5*	6.4	l. 7.3* r. 6.4*	6.5*	5.5	6.4	–	7*
	width	4+	4.8–5.0	5.1	l. 5.4* r. 5.1*	4.8*	–	7.0	–	–
	height, ext.	6–	6.0	6.3	–	–	–	–	–	–
m_1	length	7	8.5–9.0*	8.5	9	7.4*	9	7.5	–	5.8
	width	6.6*	6.3–6.5*	a. 6.3 p. 6.2	6.1*	6.0*	–	–	–	5.2
	height, ext.	5	5.1*	4.8	–	–	–	–	–	–
m_2	length	10	9.2–9.7*	10.2	11	8.9*	10	9.5	–	6.6
	width	7.1*	6.6–7.0*	a. 7.6 p. 7.3	a. 7.8* p. 7.6*	7.1*	–	7.0	–	5.9
	height, ext.	6	6*	7.3	–	–	–	–	–	–
m_3	length	12	11.3–12.9	11.7	15*(?)	–	–	11.5	13.4	–
	width ant.	7.8*	7.0–7.5*	–	7.5*	–	–	7.0	9.8	–
	width post.	7.5*	6.6–7.1*	7.5	7.4*	–	–	–	–	–
	heigth, ext.	6.0	–	–	–	–	–	–	6.0	–

The measurements marked with * have been taken from the figures. The measurements of m_1 and m_2 of *Inuus florentinus* Val d'Arno cf. Ristori mentioned by BERNSEN (1931, p. 69, last column of lower Table) must have been taken from RISTORI's figures too, as the latter does not mention them in the text.

tooth appears to be slightly less compressed from side to side. A broad faint groove occurring on the lateral side of the recent tooth is absent on the tooth from Tegelen.

Perhaps these differences are due to the fact that the fossil tooth is not that of a very strong individual, as in some recent male skulls, smaller than that mentioned above, the lateral groove is also missing, and the tooth is more compressed laterally. A linear, narrow (width 2.5 mm) wearing-facet runs all along the inner side of the sharp posterior edge of the crown where it meets the low, but elongated, crown of the anterior premolar of the lower jaw.

Besides this canine from Tegelen it is only of *Mac. robusta* (Young) that a fossil upper canine of a *Macaca* is known. The Chinese tooth is considerably shorter. In the text YOUNG (1934) mentions a maximal height of 37.0 mm. As regards the crown (YOUNG, fig. 50A) the shortness may be due to the advanged stage of wear, but it is also the root which, measured at the figure, is much shorter (viz. 9.0 mm) than in the canine from Tegelen. Moreover, the Chinese tooth is less compressed from side to side, and thus looks a less fierce weapon than that of *Mac. florentina* from Tegelen.

From both the upper premolars the inner root has been broken off at the base, but the outer roots are undamaged. In p³ the latter are almost cylindrical, and short, diverging from each other and showing between them an accessory rootlet broken off very near to its base. In p⁴ the roots are compressed from the front backward, much longer, and not diverging; there is no accessory rootlet.

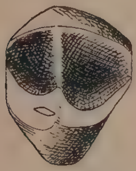


Fig. 13. *Macaca florentina*, Tegelen. P⁴ sin., crown-view 3 ×.

The crown of the premolars exists in one pair of cusps which stand opposite to each other, connected by a transversal crest, at both sides of which a little basin is surrounded by a shelf or wall which forms the anterior, and the posterior side respectively of the crown. Both premolars are moderately worn. The outer cusp of p³ shows a wearing facet along its anterior and posterior slopes. The posterior shelf has been so much attrited, that it shows an islet of dentine in the middle. A small sharp notch separates this shelf from the inner cusp.

Also p⁴ (fig. 13) displays distinct wearing facets, namely along

Measurements of upper premolars and of m^2 in fossil *Macaca*

	Mac. florentina		*Mac. pliocena*	*Mac. sylvana* recent		*Mac. anderssoni*	*Mac. robusta*	*Mac. suevica*
			Owen 1846	Leiden	Stuttgart	Schlosser 1924	Young 1934	Freudenberg 1932
	Tegelen		Grays Thurr.	cat. a	4 ex.	Mien-chih-hsien	Choukoutien	Heppenloch
p^3 1. length	5.6			5.7		11**(6?)	5.0	5.1
p^3 2. width	6.9			6.8		8?	6.3	5.8
p^3 2 : 1	1.23			1.19	1.14–1.31	1.33?	1.26	1.14
p^4 1. length	5.6			6.0		6.0	5.7	5.6
p^4 2. width	7.1			7.5		8.5	7.0	6.8
p^4 2 : 1	1.27			1.25	1.17–1.31	1.42	1.23	1.21
	Gundersheim Heller 1936	Val d'Arno Ristori 1890		cat. b				3 ex.
m^2 length	11	10.1*	9.4*	10	9.4–10	10	9.5	9.6–9.8
m^2 width, ant.	10.6	10.1*	9.4*	9	8.4–9.3	10.5	7	8.7–9.1
m^2 width, post.	9.7	9.9*	–	8.4	8.1–8.5	–	–	8

* Measured on the figures.

** This number must be a misprint, as the figures show that the length of p^3 is practically equal to that of p^4.

the hind slope of the outer as well as of the inner cusp. The anterior slope of the latter is so far worn off that an islet of dentine has come into being near the top of the cusp. Just as in *Cercopithecus* (?) *asnoti* Pilgrim (1915, Pl. 1, fig. 2) the portion of the crown lying posterior to the transversal summit of the crest is distinctly larger than that anterior to it. This is in contradiction to Pilgrim's assertion, that "In *Macacus* the two distances are the same". So far as I can judge from the skulls of recent *Mac. sylvana* which I saw, the posterior portion of p^4 is often larger than the anterior, although less so than in the Tegelen tooth.

Upper molars have not been preserved from Tegelen, and thus none of upper teeth from Tegelen can be compared with *Macaca* from Val d'Arno, as only one upper tooth is mentioned from there, being a second molar (Ristori, Pl. VIII, figs. 17–19). Also the tooth of *Macaca* cf. *florentina* from Gundersheim, recorded by Heller (1936), is a second upper molar.

It is of *Macaca anderssoni* (Schlosser) from Mien-chih-hsien, that both upper premolars of the right side are present in the fragment of skull which is the sole record described and figured of this species by Schlosser (1924). As regards the "fragment of upper jaw with P to M^3 and some isolated teeth" from Choukoutien, Loc. 2, referred first to *Mac.* cf. *andersoni* Schloss. by Young (1932), but afterwards (1934, p. 128) termed "*Mac.* spec. Young", neither description nor figures have been given. The upper dentition of Hedinger's *Inuus suevicus* (1891) has been broken off just before the premolars, owing to which the canine and the incisors have got lost, but premolars and molars are present. Freudenberg (1932) recorded again two upper molars (m^1 and m^2) of this Heppenloch-monkey. Berckhemer (Freudenberg, p. 130, etc.) has measured the teeth and those in four skulls of recent *Mac. sylvana*. When we compare his measurements and those of both Chinese species of *Macaca*, given by Schlosser and by Young, with the premolars from Tegelen, we see that there is great agreement. Not only the fossil Italian Macaco, but, according to Hedinger, also the monkey of the Heppenloch resembles *Mac. sylvana* "ganz genau". This was also the conclusion of experienced palaeontologists, like Forsyth Major and Schlosser, who saw the Heppenloch-jaw in the Stuttgart-Museum.

Although Schlosser found in the skull-fragment of the Chinese monkey "no essential differences to skulls of the larger species of the genus *Macacus*", he thought the relative breadth of the upper premolars to be a primitive character of the former. From BERCKHEMER's measurements, however, it is apparent that the width of variety is rather great as regards the relative width in the recent premolars, and where the number of this value in the Tegelen Macaco, as well as in that from the Heppenloch fall within this width, there can be little question of a primitive character.

When SCHLOSSER, in 1888, published his Report on fossil monkeys, the following fossil species of *Macaca* were known:

I. *Mac. pliocaena* (Owen). This species is based (OWEN, 1845, 1846) upon a right maxillary fragment with m^2 (1846, p. XLVI), gathered at Grays Thurrock, in pleistocene deposits in the Thames-Valley. The tooth has been much worn off, but, according to F. MAJOR (1872), "cette dent possède la forme générale et la mode d'usure qui caractérisent le *Macacus* et le distinguent du *Semnopithecus*, etc." No measurements of this tooth have been published.

II. *Mac. prisca* (Gervais), from the "marnes fluviatiles pliocènes" de Montpellier is a right mandibular fragment with p_3–m_2, two canines, and an incisor (GERVAIS, 1859, p. 11, figs. 4 and 5). The size is that of *Mac. sylvana.* The length of p_3–m_2 is 30 mm. There is no trace of a cingulum on the molars. GERVAIS laid stress on the fact that it is neither a Semnopithèque nor a Cercopithèque and GAUDRY (DEPÉRET, 1890, p. 17) who saw the specimen in Paris, thought it to be a true *Macaca*.

III. *Mac. sivalensis* (Lydekker, 1878) from the Siwalik Hills, based on two fragments of upper jaws, the right one with hardly worn m^1 and m^2, and m^3 in the alveole, the left with the unworn m^3 and the broken bases of p^4–m^2. It is certainly a *Macaca*, but much smaller than both species mentioned above.

In 1915 PILGRIM described and figured a right mandibular fragment with well worn p_4–m_2 from the same locality, and of corresponding size, and thus referred it to *Mac. sivalensis*. He pointed to some affinity of this species with *Dolichopithecus*. It is apparent from our Table (p. 180) that the lower molars of *Mac. sivalensis* are rather small, but that p_4 is longer than in both other species mentioned there.

IV. *Mac. florentina* (Cocchi). It appears that SCHLOSSER (1888) was not acquainted with COCCHI's publication of 1872, with his clear description and figures; at least he does not mention it, and writes: "Bis jetzt noch nicht genauer beschrieben".

In 1914 STROMER gave a list of the literature regarding fossil Cynopithecidae published later than 1888. The following new forms of fossil *Macaca* had been recorded in those years:

V. *Mac.* (= *Inuus*) *nemestrina* nov. mut. *saradana*, from the Kendeng-deposits of Java, was recorded by DENINGER (1910), who described under that name a left mandibular fragment with p_3–m_3 from deposits somewhat younger than the *Pithecanthropus*-deposits. This fossil monkey falls within the width of variation of *Mac. nemestrina* and stands the latter "ausserordentlich nahe".

VI. *Mac. tolosana* (Harlé, 1892), gathered in a "repaire de Hyènes" à Montsaunès, a pleistocene cave near Toulouse, is based upon a right mandibular ramus with p_4–m_2; the promised figures seem never to have been published. The length of p_4 and of m_2 appear to be that of Cocchi's type of *Mac. florentina*; m_1 is 9 mm long and thus 2 mm longer than in the latter.

VII. *Mac.* (= *Inuus*) *suevica* (Hedinger, 1891). Fragment of maxillae with premolars and molars from the pleistocene Heppenloch (Schwäbische Alb, Württemberg).

VIII. *Mac.* spec., from the Upper Freshwater Bed of West-Runton, based upon the distal extremity of a humerus described and figured by Hinton (1908).

IX. *Mac. trarensis* (Pomel, 1896) is the term applied to some extremity-bones from pleistocene deposits in Algeria.

Since Stromer's list, China and Europe have produced further fossil records of *Macaca*:

X. *Mac. anderssoni* (Schlosser, 1924) from Mien-chih-hsien, consisting of an upper jaw with dentition.

XI. *Mac. robusta* (Young, 1934) from Choukoutien, represented by some upper and lower jaws with dentitions.

XII. The European remains are scanty. Two upper molars from the Heppenloch (Freudenberg, 1932) certainly belong to *Mac. suevica* (Hedinger). The other remains (a lower jaw with worn-off dentition from the Tegelen Clay (Bernsen, 1930), an upper molar from Gundersheim (Heller, 1936), and some specimens from Hungary and Transylvania (merely mentioned by Kormos, 1937) all found in Villafranchian faunas have been provisionally termed *Mac.* cf. *florentina* (Cocchi). It is probable that the proximal half of an ulna from synchronous deposits in Senèze (Haute-Loire), indicated by Stehlin (1923) as *Macacus* spec., belongs to the same species. Unfortunately, limb-bones have never been recorded from Val d'Arno. Roman (1935, p. 54) mentioned among "des dentitions de singes" in the Museum at Lyons *Macaca prisca* from Montpellier, bequeathed by the late Mr. Mauche of that place.

Perhaps, also the geologically somewhat younger English *Macaca* from Grays-Thurrock and from West-Runton may be referred to this species, which must have been closely related to the recent *Macaca sylvana* of the Gibraltar Rock and North-west Africa.

Where the fauna of Montpellier, in which the jaw-fragments of *Mac. prisca* (Gervais) have been gathered, has so much in common with the Villafranchian faunas, (Pilgrim, 1938, p. 445) it is not improbable that there has been but one European fossil species of *Macaca*, which lived there in the Astian of Montpellier through the Villafranchian and Lower-Cromerian (= Lowermost Pleistocene, or Upper-Pliocene according to other authors) met with in Val d'Arno, Tegelen, Senèze, Beremend, and Gundersheim, but also later, together with advanced species of *Mimomys* in Upper-Cromerian times (Püspökfürdö, West-Runton). In the Clacton-stage of the High-terrace in the Thames-Valley it was accompanied by primitive *Arvicola*, *Hippopotamus*, *Rhinoceros megarhinus* (= *mercki*), *Elephas antiquus*, etc. (Grays-Thurrock).

The geological age of the Heppenloch monkey, and of that from the Hyaena-cave in Montsaunès, may be still somewhat younger, but these faunas are not yet sufficiently well known as to allow of an irrefutable establishment of their age (Kormos, 1937 and Heller, 1939, p. 16). From the Heppenloch Freudenberg mentioned *Bison*, *Elephas primigenius*, *Felis spelaea*, *Cuon alpinus*, *Sus scrofa*, *Cervus elaphus*, etc., and thought the fauna of the *Hyaena*-cave to be of about the same age. He assumes a "schwindende Riss-Eiszeit und ein Steppenklima mit lokaler Bewaldung". This may perhaps apply to the occurrence of a monkey in Southern France and in Württemberg, but as for Western Europe (e.g., England and the Netherlands) it is precluded, that during or after the Riss-glaciation any monkey has lived there.

Sus strozzii Meneghini

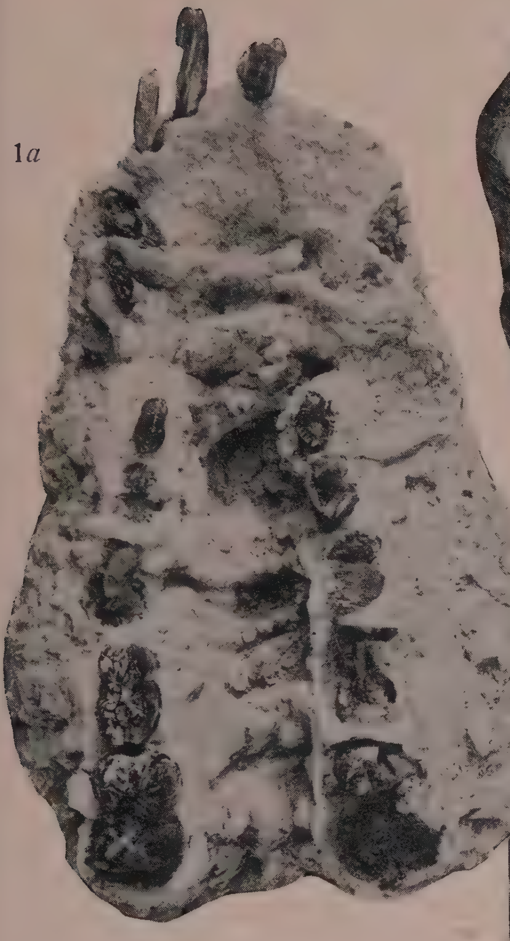
Plate III, fig. 1

In 1935 the lower jaw with nearly complete dentition of a young boar from the Tegelen Clay was added to the collection Böhmers and van Bemmel in the Zoological Museum, at Amsterdam. It had been saved by Mr. L. D. Keus, Venlo. A short description and a figure was published the following year (Schreuder, 1936).

The fossil pig of Tegelen was first made known by Richarz (1921), who shortly described some isolated teeth (i_1 and i_2 sin., both c inf., m^1, m^2 and m_2 dext., and both m_3), and afterwards by Bernsen (1931) who fully described and figured these remains, together with an upper canine,

The newly found jaw is hidden in a concretion of clay-ironstone, with the teeth protruding out of it; they are of a bluish black colour. Of the jaw only the borders of the alveoles can be observed. They are ranged in two parallel rows, with the exception of the symphysial portion of the jaw, which is some-

1*a*



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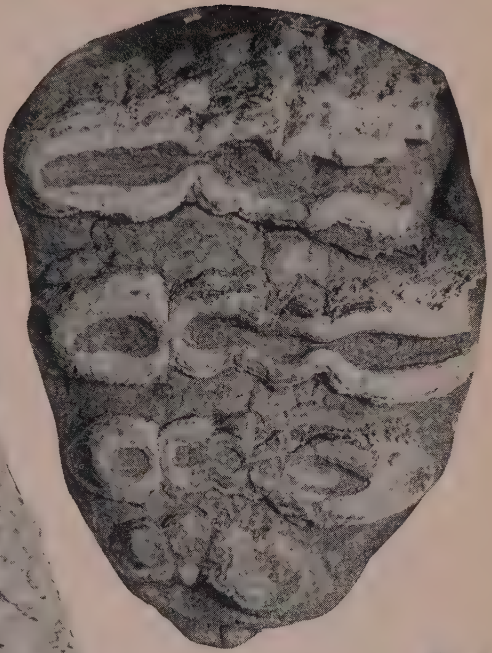

1*b*

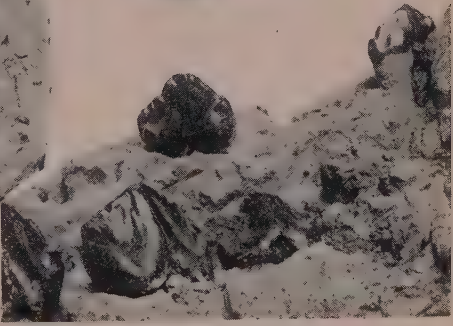

Fig. 1*a*. *Sus strozzii* Men., Tegelen. Lower jaw with i_1, id_2, c(stump), p_1, p_2, m_1, m_2 sin. and i_1, c(stump), p_2, p_3, p_4 (ant. half) dext.; $^2/_3 \times$ nat. size.

Fig. 1*b*. Ditto; part of same dentition seen from the right side; p_1 and p_2 sin, int. view and p_2, p_3 and p_4 dext., ext.; nat. size.

Fig. 2. *Archidiskodon meridionalis* (Nesti), Tegelen; posterior half of D^4 sin., crown-view; nat. size. (Same tooth text fig. 8).

what dislocated, whereby the anterior premolar (p_1) and the canine of the right side have been pushed outward. The youth of the dentition is apparent from the lack of any trace of m_3 and from the presence of the left second incisor of the milk dentition. In the recent European wild boar this stage of the dentition indicates an animal of about 18 months.

The first incisors are practically unworn. They were broken off, and a portion between the root and the crown must have got lost, as both parts did not fit well together. In this way no longitudinal measurement of the tooth can be given. The max. width, near the top, is 8.3 mm. The thickness near the base of the crown is 10 mm. They have the general form of the incisors of *Sus* (cf. STEHLIN, 1899, p. 309). The two tops, separated by a groove and the median ridge along the upper (inner) side of the crown, are distinct. The ridge ends at a distance of 3 mm from the extremity of the outer top. The top of the left second incisor can be seen in the alveole, out of which protrudes the slender milk tooth (max. width 6.0 mm). It is so much worn that the enamel covers only the buccal side and a narrow strip of the lingual side of the crown. The third incisors are not represented. Like the canines, they have been broken off at the borders of the alveoles. The typical cross-section of the canine is that of the *Sus verrucosus*-group, the posterior side being much shorter than the outer side. Naturally the circumference of these teeth with permanent growth is not great in this young dentition. The lower canines from Tegelen, described by BERNSEN (1931), are nearly twice as strong.

Also the place and the relative size of the premolars agree with the characters in question, mentioned by STEHLIN (p. 154) for *Sus strozzii*, viz. in the Tegelen dentition the distance from the canine to p_1 is short (3 mm), but that of the latter to p_2 is considerable (20 mm). The combined length of m_1 and m_2 (55 mm) divided by that of p_3 and p_4 (37 mm measured at the alveoles) is 1.49, and this is exactly the value noted by STEHLIN for this ratio.

Unfortunately, of the last premolar, the most characteristic tooth in Suidae (cf. PILGRIM, 1926), only the anterior portion has been saved in the Tegelen jaw, namely that of the right specimen. Of the left p_4 the internal cast displays three roots; the two posterior diverge considerably from each other and from the anterior one. The right p_3 is perfectly preserved, but the crown of the left specimen has got lost. P_2 of both sides is undamaged, and so is the left p_1. The right first premolar has been broken off at the base of the crown. Our Plate 1, fig. 1*a* shows the crown-sides of the left teeth; the right teeth-row has suffered a sideways pressure, so that on the figure the right premolars present display the labial surface of their crown.

The form of the premolars is considerably thicker and more elongate than in *Sus scrofa*. The unworn specimens are of the sharply cutting type. The steep, slightly convex, front-slope, as well as the less steep, straight, or somewhat concave, hind-slope of the crown, form a sharp crest interrupted, p_1 excepted, by several transverse notches which increasing in distinctness from p_2 to p_4, do not as a rule run down the sides of the crown for more than 1 mm. On STEHLIN's figure of the unworn p_2–p_4 of *Sus strozzii* from Val d'Arno, these notches have not been indicated. Due to a favorable exposure they are beautifully to be seen on p_2–p_4 dext. of our figure.

In the dentition from Tegelen the anterior premolar present (p_1 sin.) is a somewhat simplified replica of p_2 just as in *Sus antiquus major*, and by no means caniniform (STEHLIN, 1899–1900, p. 154), although the summit of the crown lies somewhat before the middle. It has a max. length of 10.3 mm and a width of 4.9 mm. The front slope displays one notch in the middle, the hind slope shows two of them, one lying at about the same distance from the top as the anterior one, the other near to the base of the crown. The outer side of the crown is slightly more convex than the inner, and in both directions. The roots stand very close together.

The second premolar (p_2) is slightly lower relatively and the top lies just in the middle of the crown. The max. length is 13 mm and the width 7 mm. The anterior slope shows one notch more than p_1, and the anterior and the posterior cingulum are distinct. The roots diverge considerably. At the inner side the anterior slope is interrupted by 5 distinct notches, all above the cingulum. From the summit the profile slopes down anteriorly at an angle of about 45° as far as to the anterior cingulum, from where it runs down almost vertically. The sharp anterior crest displays numerous very fine transverse striae caused by the laminar structure of the enamel layer.

In contrast to the two preceding teeth the posterior end of the profile of p_3 is somewhat elevated. The tooth is larger again, and somewhat more complicated than is p_2. It is the only one among the premolars which shows a distinct wearing-facet at the top and all along the posterior slope of the crest which is furnished with the traces of 7 minute notches. The anterior slope shows 9 of them. The anterior cingular cusplet is considerable, the posterior slightly less so. The max. length of this tooth is 15.5 mm, the width 10 mm. At the posterior end the cingulum forms the base of the slope, and runs there vertically down along the outer side; at the inner side it makes the cusplet mentioned above.

Unfortunately of p_4 merely the anterior half has been saved. The crest is more coarsely notched than in the preceding teeth, so that at the inner side of the tooth not more than 5 notches can be counted, some of them run faintly down the crown vertically for a considerable distance. The outer side of the anterior half is quite like that of p_3. Length and width of this tooth can not be given, but the height of the crown is 15 mm in the middle, and thus considerable more than in p_3, where it is 12 mm.

The first molar is long and remarkably narrow. The latter is apparent from our Table, where it is compared with m_1 in a recent skull of *Sus scrofa* and with *Sus lydekkeri* (ZDANSKY, 1928) from Choukoutien. The enamel pattern on the wearing surface is broken by a longitudinal crack running over the posterior, the central, and the anterior-inner, cusp. Both the inner and the outer posterior cusps are cleft by a transversal crack. The

	Sus strozzii Tegelen	*Sus lydekkeri* Choukoutien	*Sus scrofa* Het Loo
p_1 length	10.3	10.2	–
p_1 width	4.9	4.6	–
p_2 length	13.0	aver. (4 ex.) 15.2	12.6
p_2 width	7.0	aver. (4 ex.) 8.2	5.4
p_3 length	15.5	aver. (5 ex.) 15.7	14.0
p_3 width	10	aver. (5 ex.) 9.0	7.8
m_1 1. length	21.7	18.5	16
m_1 2. width	13.4	13.4	12
m_1 1 : 2	1.62	1.38	1.33
m_2 1. length	28	aver. (5 ex.) 25.3	21
m_2 2. width	20	aver. (5 ex.) 16.8	15
m_2 width m_1 : w.m_2	1.49	1.25	1.25

tooth is moderately worn, but not yet so much that the six main cusps have fused. In the transverse valley there is a cingular cusp (tubercle) at the outer side, in the inner there is none. The anterior cingulum is distinct as regards its inner portion which bears a tubercle; the outer portion has been worn off by the neighbour tooth. The strong posterior cingulum bears the posterior cusp.

M_2 has hardly been worn. This tooth also has been cleft by similar cracks as in m_1. Small wearing-facets occur at the tops of the anterior pair of cusps and at the central cusp. The cingular tubercles along the anterior and the longitudinal sides of the crown are stronger than those of the first molar.

The pig of Tegelen has long been the sole record of *Sus strozzii* in Europe outside Italy; I was therefore greatly interested when Professor STEHLIN, in 1937, wrote me: "Vielleicht interessiert es Sie, dass *Sus strozzii* von dem in Tegelen die ersten Spuren nordwärts der Alpen zum Vorschein gekommen sind, nun auch in der Auvergne nachgewiesen ist, und zwar in Senèze, von wo wir diesen Winter ein ganzes Skelett desselben erhalten haben." This fact is a new proof of the great resemblance between the Tegelen fauna and those of Senèze and the Upper Val d'Arno.

Sus strozzii belongs just as *Archidiskodon meridionalis* and *Leptobos* to the invading forms among the Tegelen assemblage. They came from Asia and first appear in Europe in the Villafranchian.

Comparison of the Tegelen fauna with other Villafranchian assemblages

As regards the facies-character of the Teglian it is the lacustrine strata of the upper portion of the Arno Valley which most resemble the fluvio-limnic deposits of Tegelen. The Val d'Arno superiore stretches from Arezzo in North-western direction, being a wide plain between two spurs of the Apennines, with the form of a lake. This plain is ploughed up by narrow gorges with steep slopes, forming continuous sections of enormous extent in the mammaliferous lacustrine deposits. Here a lower fauna with *Anancus arvernensis* is to be distinguished from an upper fauna in which merely *Archidiskodon meridionalis* occurs (cfr. SCHLESINGER, 1922, p. 216, etc.). It is with the latter Upper Villafranchian fauna that the Tegelen fauna most agrees. It is to be regretted that the local situation makes it impossible to gather the earlier and the later portion of the Italian fauna separately. Therefore in our Table it is given as a whole conform to the lists of Major, Weithofer and Mayet et Roman.

As regards the latitude, as a matter of course the English strata are better suited to a comparison with the Teglian, the more so as they are deposits of the same river-system. However, the English strata are fluvio-marine, littoral or estuarine, and partly have suffered disturbance by which the fossils may have been removed. Moreover the deposits are sandy for the greater part, and, besides the land-mammals and freshwater shells, many sea-shells and bones of sea-mammals have been found in them.

Although the Tegelen fauna has been introduced by Eug. Dubois (1904*a*) as being an equivalent of that of the Cromer Forest Bed, this author wrote as early as 1905(*a*): "Il est probable que l'Argile de Tegelen . . . . soit réellement un peu plus ancienne que le Cromérien". This is also the inference of Cl. and El. Reid (1915, p. 8), after a careful analysis of the Tegelen flora, which, according to them is: "newer than the . . . . Amstelian, and probably represents the Norwich Crag". Also my study (1936*c*) of the Voles led me to term the Tegelen Clay synchronous with the Norwich Crag.

Kunst's assumption (1937, p. 113) that the Clay of the Kempen, which yielded the remains of *Cervus falconeri* is related to that of Tegelen in the same order as the Norwich Crag is to the Cromer Forest Bed, I can not share, if there is meant something else than that the Kempen Clay in question is somewhat older than the Tegelen Clay. Kunst based her opinion merely on the occurrence of the species of deer. A glance at the whole list of the Tegelen Mammals reveals at once that this fauna is distinctly older than that of the Cromer Forest Bed which was formed during the Günz-Mindel Interglacial. Typically Villafranchian species, as *Mimomys pliocaenicus*, *Mim. newtoni*, *Hystrix* cf. *etrusca*, *Crocuta perrierii*, *Sus strozzii* and *Leptobos*, do not appear in the Forest Bed. On the contrary *Hippopotamus*, *Megaceros*, *Cervus elaphus*, *Bison* and more evoluated Voles, as *Mim. intermedius*, are absent in Tegelen, but are characteristic of the Günz-Mindel Interglacial.

The clay of the Belgian Kempen and the denuded layers in the mouths of the Scheldt, which, too, yielded the remains of *Cervus falconeri* are somewhat older than the Tegelen Clay and may be formed shortly before or in the very beginning of the Günzian period. That clay of the Kempen and of the Scheldt-

Lists of some Villafranchian Faunas

Val d'Arno superiore	Senèze	Tegelen	Norwich Crag
Macaca florentina	*Macaca* spec.	*M. florentina*	—
—	*Dolichopithecus arvernensis*	—	—
Machairodus nestianus	—	—	*Machairodus?*
Machairodus cultridens	*M. cultridens* 3)	—	
Machairodus crenatidens	*M. crenatidens*	—	
Felis issiodorensis		—	—
Felis arvernensis	*Felis* spec.	—	—
Felis etruscus		—	—
—	—	—	*Lutra reevi*
Canis megamastoides	*C. megamastoides*	—	*Canis* spec.
—	—	—	*Canis lupus*
Crocuta perrierii	*Cr. perrierii*	*Cr. perrierii*	—
Crocuta robusta	—	—	—
—	*Hyaena arvernensis*	—	*Hyaena striata*
—	—	—	*Hyaena antiqua*
Ursus etruscus	*U. etruscus*	*U. etruscus*	—
—	*U. arvernensis*	—	—
—	—	*Pannonictis pilgrimi*	—
—	—	*Pannonictis pliocaenica*	—
Equus robustus	*E. robustus*	*E. robustus*	*E. robustus*
Equus stenonis	*E. stenonis* 3)	—	—
Tapirus arvernensis	—	—	—
Dicerorhinus etruscus	*D. etruscus* 3)	*D. etruscus*	*D. etruscus*
—	—	*D. merckii*	—
Mastodon borsoni	—	—	—
Anancus arvernensis 1)	—	—	*An. arvernensis* 1)
Archidiskodon meridionalis 1)	*A. meridionalis* 3)	*A. meridionalis*	[illegible]

			—
Castor fiber	—	*C. fiber*	—
—	—	*Trogontherium boisvilletti*	*T. (boisvilletti?)*
Hystrix etrusca	—	*Hystrix* cf. *etrusca*	—
Lepus vald'arnensis		—	—
Lepus etruscus	*Lepus* spec.	—	—
—	—	*Hypolagus brachygnatus*	—
—	—	*Desmana tegelensis*	—
—	—	*Talpa (praeglacialis?)*	—
Mimomys pliocaenicus	*M. pliocaenicus*	*M. pliocaenicus*	*M. pliocaenicus*
—	*M. newtoni*	*M. newtoni*	*M. newtoni* (in Weybourne Crag)
Eucladoceros dicranius	—	*E. dicranius*	—
Eucladoceros ctenoides	*E. senezensis*[3]	*E. tegulensis*	*E. sedgwickii?*
	E. darestei[3]		
Cervus perrieri			*Cervus falconeri*
	Cervus philisi[4]	*C. rhenanus*	*Cervus suttonensis*
Cervus spec.			*Cervus carnutorum*
			Cervus verticornis
Gazellospira torticornis	*G. torticornis*	—	*Antilope* spec.
—	—	—	*Gazella anglica*
—	—	—	*Gazella daviesii*
Naemorhedus philisi	*N. philisi*[4]	—	—
—	*Procamptoceras brivatense*	—	—
—	*Deperetia ardea*	—	—
—	*Megalovis latifrons*	—	—
—	*Alces latifrons*[3]	—	*A. latifrons* (in Weybourne Crag)
Leptobos etruscus	*Leptobos elatus*[3]	*Leptobos* cf. *elatus*	—
—	*Ovis* spec.	—	—

[1] As to the much discussed possibility of coëxistance of these two Proboscidae see: SCHLESINGER 1922, p. 215 etc.

[2] See p. 173.

[3] A complete mounted skeleton is exposed in the Museum at Lyons (ROMAN, 1935, p. 9).

[4] A complete skeleton is present in the Museum at Basle (STEHLIN, 1923, p. 276, and SCHAUB, 1941).

mouths may be related to the Tegelen Clay like the lowest strata of the Norwich Crag are related to the higher, and the older portion of the Val d'Arno fauna is related to the younger, and as the fauna of Perrier is to that of Senèze.

Tesch's point of view is (1934) that the base of the English Norwich Crag is synchronic wiht the cold phase occurring in the marine layers (II om of the map) beneath the Tegelian. In both deposits occur several "cold" molluscs, viz. *Astarte borealis*, etc. These cold deposits of the Icenian sea form the middle third portion of the Icenian in the Netherlands. The marine Icenian is covered by the terrestrial Tegelian which is synchronic then with somewhat higher layers of the Norwich Crag.

Comparing the faunal assemblages from Tegelen and from Senèze, we must bear in mind, that as a matter of course *Trogontherium*, *Castor* and *Desmana*, three species which are bound to a river-life, do not occur in Senèze, where the strata point to a deposition, after a vulcanic eruption, in a rather small lake, where the animals from far and near came to drink. The comparison of the mammalian assemblages of Tegelen and Senèze is impeded by the fact that neither Antelopes nor Felidae or Canidae have hitherto been found in Tegelen. Representatives of these Carnivores must undoubtedly have lived there, but as for the Antelopes it may be that they had already disappeared from the high latitude of Tegelen (51°), when in Senèze (46°) there lived still as much as five species.

Mayet et Roman's words exactly fit the case of the Tegelen fauna. "Senèze c'est un horizon de la seconde partie du Villafranchien se plaçant dans les derniers millénaires de Chagny, de Perrier, du Villafranchien d'Italie."

The large horse of Tegelen, *Equus robustus* Pomel, also lived in Senèze, but the smaller horse of Senèze, *E. stenonis*, has not yet been found in Tegelen, nor in the Norwich Crag (Hopwood, 1936).

The large deer of Tegelen, *Euclodoceros tegulensis* and the small three-tined deer, *Cervus rhenanus*, find their analogues among the fauna of Senèze in the large *Eucladoceros senezensis* and (or) *darestei*, and in the small *Cervus philisi* (Schaub, 1941, *a* and *b*). According to Teilhard et Piveteau (1932) the small deer of both localities are identic, an assumption neither denied by Bernsen (1934), nor by Kunst (1937, p. 92). Schaub estimates this small deer which is characteristic of the Upper Villafranchian, nearer related to the Manchurian *Sika* than to *Rusa* of the Moluccas. (The extremities of the long bones from Tegelen are distinctly less broad (BERNSEN, 1934) than those of the type of *C. philisi* (SCHAUB, 1941*b*)) When both species are identic indeed the name of *rhenanus*, given by DUBOIS, in 1904, must prevail over that of *philisi* applied by SCHAUB in 1941. In both localities the deer are numerous, much more so than the ox, *Leptobos*. The tapir, occurring in the Upper Val d'Arno as well as in Perrier, Coupet, Vialette, etc., has not been found in Tegelen and in Senèze, nor in the Norwich Crag. It is known from the geologically somewhat older Red Crag. At the time when the Tegelen fauna lived the antelopes and the tapir, as well as *Mastodon*, probably had already retired to lower latitudes. If the remains of *Mastodon* 1) in the Chillesford Crag have not been derived from older strata, the animal must be considered to have been a relict there, since the faunas of Tegelen and of Senèze, which are very probably even somewhat older than the Chillesford Crag, do not count this Proboscide among their components, but *Archidiskodon meridionalis*.

On stratigrafical grounds, viz. the presence of a thick layer of gravel beneath the clay in Tegelen, its fauna has from the first been placed in an interglacial period. DUBOIS, who thought the glacial period in which the gravel has been laid down to be the Mindel-glaciation, termed the Tegelen Clay Mindel-Riss-Interglacial, although Pliocene. TESCH (1937) places the Teglian after the Günz-Glacial which he terms "de eerste glaciale phase". Thus the Tegelen Clay is taken by TESCH to be Günz-Mindel-Interglacial. In my opinion there is much to be said for terming the first glacial phase "Günz I" and the Tegelen Clay "Günz-Interstadial".

Saint-Prestian faunas, such as those of the Forest Bed, Mosbach (Hauptfauna), Mauer, etc., lived during the long Günz-Mindel Interglacial, but Villafranchian assemblages, such as those of Senèze, Norwich Crag, Upper Val d'Arno and Tegelen, are undoubtedly of Günzian age. German palaeontologists as ZEUNER and HELLER share my opinion. ZEUNER (1938, p. 32):

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1) "This skeleton, of wich so circumstantial an account has been given by the Rev. Mr. LAYTON, is stated to have been found on the surface of a bed of marl, "between the chalk and gravel", at Horstead, without indicating the precise relation of the bed to the Crag and the superincumbent blue clay or submerged forest-bed." (FALCONER, 1857, p. 347).

"... lässt es mich für wahrscheinlich halten, dass Tegelen Günz I–Günz II vertritt." And HELLER (1938, p. 52): "Durchaus abwegig erscheint mir die Altersdatierung der Tegeler Tone, die nach TESCH günz-mindel-interglacial sein sollen".

ZEUNER (1937) relying on BOSWELL's studies of the Mollusca of the Crags observed two cold phases in Crag times, viz., in the Newer Red Crag and in the Weybourne Crag [1]), which he correlates tentatively with the two cold phases of the Alpine Günz. On the other side of the North-sea, in the Netherlands, two regressions of the sea have been stated in Crag times, viz. in the Amstelian and in the period of *Viviparus glacialis*. Both periods are fairly well synchronous with the Newer Red and the Weybourne Crag respectively. Could not then the transgression of the Icenian sea be caused among others by the melting of the icesheet of the Günz I?

I propose tentatively the following scheme (p. 197) based upon the newer views of English and German palaeontologists, involving in it the Dutch conditions come to our notice during the last years, by the valuable investigations for the Geological Map of the Netherlands.

A comparison of the Tegelen fauna with an approximately equivalent fauna from Gundersheim, termed "oberpliocän" by HELLER (1936) and almost synchronous with the Villafranchian assemblages treated above, presents more difficulty, as the animals of which the remains have been gathered did not perish on the borders of rivers or lakes, but, as a rule, did fall a prey to the carnivorous mammals and birds (owls) which inhabited the fissures, crevisses and caves of the limestone-plateau, near Gundersheim, in Lower-Cromerian (Crag) times. The absence of any remains of Ungulates renders it a matter of great difficulty to compare them with the classic faunas of which just the Micromammalia (which are predominant in Gundersheim) have been practically overlooked. HELLER mentions as many as 7 species of Insectivores, 13 of bats, and 12 of mice and voles. The monkey, the hyaena, the hare, and the voles of Tegelen also occurred at Gundersheim. Perhaps the "Mustelide" is, like in Tegelen, *Pannonictis*. HELLER assumes the assemblage of Gundersheim to be a "Grassteppenfauna".

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[1]) DUBOIS (1905*b*), after a visit to Norfolk and Suffolk in the company of REID, wrote: "Que le Crag de Weybourne .... soit un dépot glaciaire, personne n'en doute."

Correlation scheme of Plio-Pleistocene formations in England and the Northwestern part of the Continent, based on the mammalian faunas and on glacial phenomena

	East-England	Continent
Mindelian { Mindel II Interstadial Mindel I	Older North-Sea drift.	Süssenborn Mosbach III Mauer
Günz-Mindel Interglacial	Cromer Forest Bed (Cromerian) { Bacton West Runton East Runton	Mosbach II (Hauptfauna) Jockgrim, Eberbach Saint-Prestian, with *Archidiskodon meridionalis*, recent type
Günzian { Günz II	Weybourne Crag	Mosbach I Gundersheim
	Chillesford Crag	Regression of the North-Sea (mouth of Dutch river in England)
Günzian { Interstadial	Norwich Crag	Tegelian or Upper-Villafranchian (Tegelen, Senèze, etc.) with *Archidiskodon meridionalis*, archaic type Icenian (Transgression of the North-Sea)
	—·—·—·—·—·—	—·—·—·—·—·—
Günzian { Günz I	Newer Red Crag	Calabrian or Lower-Villafranchian (Perrier, Chagny, etc.) with *Anancus arvernensis*, *Archidiskodon planifrons* Amstelian (Regression of the North-Sea)
	Waltonian Crag	Scaldisian

—·—·—·— Limit between Plio- and Pleistocene, after Tesch.

The extraordinarily rich Mammalian fauna from equivalent deposits in Southern Hungary (Villányer Gegend) with which the name of Dr. T. KORMOS is indissolubly bound, is of a similar provenance as that of Gundersheim. Thousands of bones in an ossiferous breccia form the remains of the diet of carnivores which found a "convenient dwelling" in a cave formed originally by a crack in the limestone. Here the Micromammalia are also predominant. In his list, KORMOS (1937) enumerates 13 species of Insectivores, 9 species of bats, 22 of Rodents etc. Fortunately, here larger mammals, too, have been gathered, and their relation to the classic Villafranchian has been amply discussed. KORMOS insists on the Upper-Pliocene age of this fauna, but STEHLIN (in STEHLIN et DUBOIS, 1932–'33) and SCHAUB (1932) term the assemblage Lowest-Pleistocene, although, according to SCHAUB, it is surprising that in this fauna genera of antelopes (*Procamptoceras* and a Tragelaphine) are present, which had hitherto only been recorded from Upper-Pliocene deposits, such as Val d'Arno, and Perrier, inc. Senèze. MOTTL (1941) terms it Saint-Prestian.

It is regrettable that of this highly interesting Hungarian fauna merely some groups have been described hitherto. KORMOS, in 1932, treated of the Felidae and the Canidae; in 1934, of the Mustelidae, the Hares and *Manis*, and, in 1938, of the Watermoles. SCHAUB (1933) described the Ruminantia. For the rest, as regards the comparison of this assemblage with other Villafranchian faunas we must depend upon KORMOS' list of names.

Most of the Tegelen mammals occur in the "Villányer Gegend" also, but some important species of Tegelen, also present in Val d'Arno and Senèze, viz. *Ursus etruscus*, *Crocuta perrierii*, *Equus robustus* and *Sus strozzii* have not been recognized there. *Alces*, besides from the Villányer Gegend, is also known from Senèze (ROMAN et DARESTE, 1931) and from the Weybourn Crag. So we may expect the elk to be found also in Tegelen some day. The remains hitherto gathered in the Netherlands are late- or post-pleistocene.

I will end with the words used by HUGH FALCONER (1857) at the end of his study on British fossil *Mastodon*: "In the preceding remarks I have confined the comparison strictly to the Mammalian Fauna. The Mollusca have unquestionably been yielded as a most powerful exponent of geological chronology, and of the successive physical changes which have taken place on the surface of the earth. But it will hardly be denied that the evidence presented by Mammalian remains, when obtained in sufficient variety and abundance, is of greater significance as a test of contemporaneous formation in geology, or the reverse: 1st, Because Mammalian genera and species are everywhere shown to be of more limited duration in time than the Mollusca; and, 2ndly, because from the vastly greater complexity of their relative functions, they are much more susceptible of being affected by the altered climatal conditions which are necessarily involved in every great physical change, and which conduce most to the extinction of species."

Summary

A historical survey of the increase of the list of Tegelen mammals precedes the description of some fossils, namely a scapula, a few upper and one lower molar, a humeral shaft and part of a horn-core of *Leptobos* cf. *elatus* (Pomel), fragments of an upper and a lower last milk molar and a large fragment of a second molar of *Archidiskodon meridionalis*, archaic form, some upper and lower teeth of *Macaca florentina*, and the young, almost complete lower dentition of *Sus strozzii*.

A comparison of the Tegelen mammals with other Villafranchian faunas leads to the conclusion that the resemblance to the mammalian assemblages of Val d'Arno superiore and of Senèze is great, and that the Tegelen Clay is a deposit of the Günzian period, and thus distinctly older than the Cromer Forest-Bed which has been formed in the Günz-Mindel Interglacial. The Tegelen mammalian fauna belongs to the Upper-Villafranchian, and most probably lived in the Günz-Interstadial.

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THE INFLUENCE OF TEMPERATURE UPON GAS-EXCHANGE IN FISH

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Much work has been done on the fact of the increased velocity of biological processes in accordance to the rise of temperature. In earlier days it was considered interesting to find out whether this relation could be expressed by means of the temperature coefficient (Q_{10}) of VAN 'T HOFF's formula or not.

If so, Q_{10} might be expected to have a practically constant value of about 2 or 3 over a comparatively wide range of temperature. Now it has already been demonstrated by KROGH a.o. on several subjects that increase of temperature, following an algebraic progression, is not accompanied with an increase in velocity of reaction in geometrical progression. In other words: the Q_{10} is not a constant value in biological processes (KROGH, 1914*a*; 1914*b*; JOHANSEN and KROGH, 1914). In general terms VAN 'T HOFF's equation does not hold for biological processes.

Many investigators have tried to express the correlation between velocity of lifeprocesses and temperature by means of μ, the temperature caracteristic in the formula of ARRHENIUS:

$$\mu = \frac{4{,}6\ T_1 . T_2 \log \frac{k_1}{k_2}}{T_1 - T_2}$$

But the value of μ proved to be nearly as inconstant as Q_{10}, though it seems preferable to use this caracteristic, since the range of variation is smaller (KRÜGER, 1940). Sometimes μ shows a fairly constant value up to a certain critical temperature, above which another value of μ can be estimated for the process, also nearly constant for a rather wide range of temperature.

This fact is explained by assuming that up to the critical temperature the process is ruled by a certain enzymic reaction with the first value of μ as caracteristic, but passing this critical temperature another enzymic reaction of the system becomes the limiting factor, with another caracteristic value of μ (CROZIER, a.o.).

The same line of thought is found in the explanation of the fact that an optimal temperature is to be observed in some biological processes (POTONIÉ, 1924). From the optimal temperature, other enzymic reactions start to counteract the first ones.

In an earlier paper, dealing with the influence of several factors on gas-exchange in fish, we already published a brief summary of the bibliography on the influence of temperature on metabolic processes (PUNT and JONGBLOED, 1943). We showed that there was no uniformity of opinions as to this relationship. We also recorded our own investigations on goldfish, determining the gas-exchange at several temperatures by use of a new method, in which CO_2-free air was pressed through the experimental vessel and the outcoming gas was analysed continually by means of the diaferometer.

The CO_2-output plotted against temperature gave a curve which showed a good deal of resemblance to the one published by EGE and KROGH (1914). But a difference was noticed: the Q_{10} showed no gradually diminishing value as described by these authors, but had a maximal value between 15° and 20° C. Both, at lower and higher temperature we found smaller values of Q_{10}.

We considered the question, whether this maximum Q_{10} might be the expression of optimal conditions to lifeprocesses in the fish at that temperature or merely the consequence of the fish being accustomed to this temperature.

In order to study this more in detail, we performed several new series of experiments.

In the first place we used tench (*Tinca tinca* L.), kept under normal conditions of temperature etc. (± 15° C). Tench lends itself particularly well for this purpose being a very quiet fish, which shows almost constant values of CO_2-production and O_2-consumption at constant feeding etc.

Gas-exchange estimations were also performed on *Cichlasoma bimaculatum* (L.), a tropical perciform fish, usually living at a temperature of ca. 25° C.

In the third place we kept tench for several weeks at higher

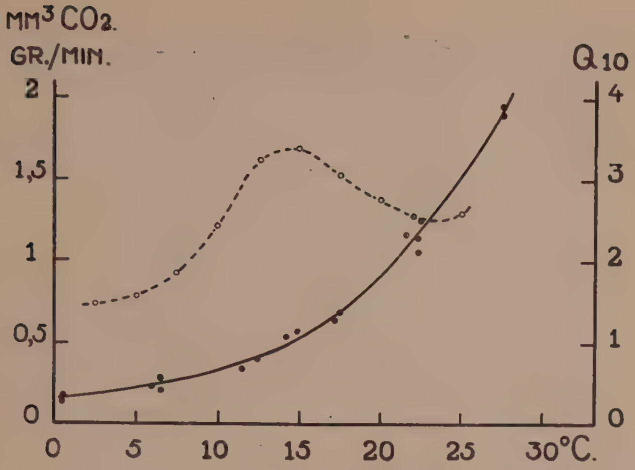

Fig. 1. CO_2-production at different temperatures, tench I, under normal conditions. Dotted line: Q_{10}.

temperatures, e.g. 25° C, trying to move the Q_{10} maximum to a higher temperature range.

In all these experiments the gas-exchange was determined at different temperatures, after giving the fish during several hours the opportunity of getting accustomed to the new conditions.

As to the first 3 sets of experiments on tenches, the CO_2-output in mm^3 per gram per minute plotted against temperature shows curves as given in fig. 1, with a constantly sloping line.

If Q_{10} values are calculated for overlapping temperature-ranges of 5 degrees, using the formula:

$$Q_{10} = \left(\frac{k_1}{k_2}\right)^{\frac{10}{t_1 - t_2}}$$

a maximal value for Q_{10} was found in all sets of experiments. In two of them this maximal value was found between 12.5° and 17.5°, in the third one between 10° and 15° (tab. I). In our earlier paper, the same was found for goldfish, the maximum of Q_{10} lying there between 10° and 15° C.

From a certain temperature upward in the higher, almost unphysiological regions (e.g. 25°—35°) the Q_{10} value increases

TABLE 1

Q_{10} of CO_2-production at different temperatures, tench (I-III) under normal conditions, (15 C°)

Temp. °C		Q_{10}	
	I	II	III
2,5—7,5	1.58	2.57	2.11
5—10	1.86	2.50	2.26
7,5—12,5	2.43	3.07	2.30
10—15	3.25	**3.61**	2.74
12,5—17,5	**3.41**	3.19	**3.06**
15—20	3.05	2.96	2.90
17,5—22,5	2.78	2.96	3.06
20—25	2.58	3.20	3.16
22,5—27,5	2.59	4.95	3.65

rapidly, probably owing to injuring actions of the high temperature; the fish at first becomes more active and, at prolonged duration, dies at temperatures of about 30° C.

The experiments on *Cichlasoma bimaculatum* showed a very regular CO_2-production but only little difference in Q_{10} values over the whole range of temperature. At higher temperatures

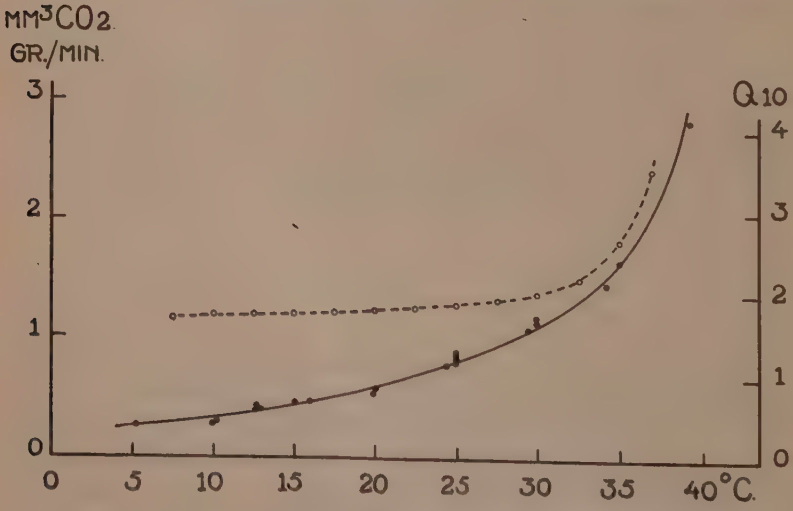

Fig. 2. CO_2-production at different temperatures of *Cichlasoma bimaculatum* (L). I. Dotted line: Q_{10}.

TABLE 2

Q_{10} of CO_2-production at different temperatures, *Cichlasoma bimaculatum* (I-II) kept under normal conditions, (25° C)

Temp. °C	Q_{10} I	Q_{10} II
5 —10	1.72	—
7,5—12,5	1.77	1.52
10 —15	1.75	1.61
12,5—17,5	1.78	1.74
15 —20	1.79	1.72
17,5—22,5	1.84	1.80
20 —25	1.86	1.99
22,5—27,5	1.91	2.16
25 —30	1.96	2.23
27,5—32,5	2.03	2.37
30 —35	2.22	
32,5—37,5	2.70	
35 —40	3.56	

only the CO_2-output was much increased and as a consequence the Q_{10} value too. The fish collapsed at 40 ° C which also happened at temperatures below 7° C (fig. 2, tab. 2).

The third series of experiments were performed on tench kept for some weeks at an environmental temperature of 25° C. Now the maximal value of Q_{10} proved to be displaced, it was found at temperatures, which lay some degrees higher than in the experiments on tench under normal conditions. (Fig. 3, tab. 3), namely between 15° and 20° C.

TABLE 3

Q_{10} of CO_2-production in tench, kept during several weeks at 25° C

Temp. °C	I	II
7,5—12,5	1.76	
10 —15	2.33	2.08
12,5—17,5	2.95	2.42
15 —20	**3.24**	**2.56**
17,5—22,5	2.70	2.34
20 —25	2.49	2.33
22,5—27,5	2.61	3.04
25 —30	2.85	
26,5—31,5	5.10	

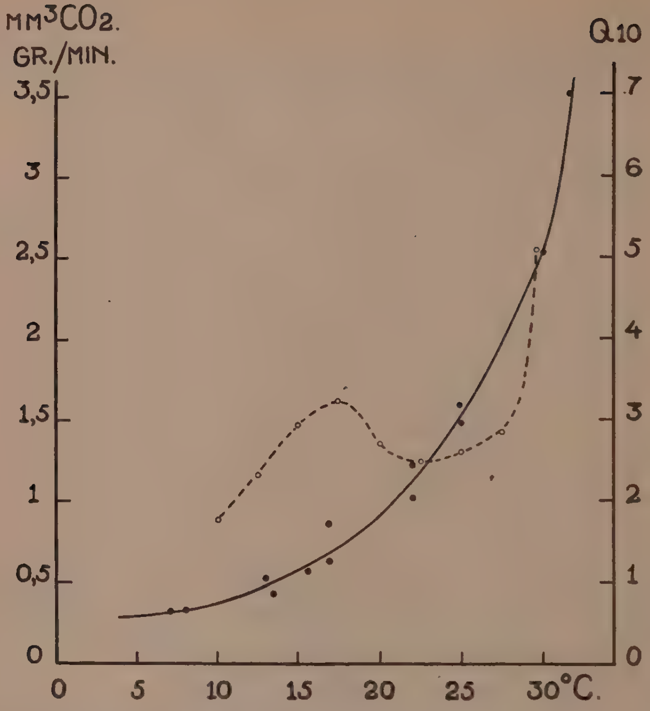

Fig. 3. CO_2-production at different temperatures, tench II, accustomed to higher temperatures. Dotted line: Q_{10}.

Discussion:

The foregoing investigations make it evident that Q_{10} has a maximum, which is found at that range of temperature to which the fish is accustomed. In other words, the gas-exchange is more dependent on temperature within this range, than at other physiological temperatures.

Potonié, 1924, who studied the gas-exchange of several animals, also claims to have found a maximal value for Q_{10} but, according to his tables, at a much higher temperature than in our experiments. But I can't agree with his manner of calculating Q_{10}, for it is not right to say Q_{10} at 42° is 4.2, when this figure represents the relation between gas-exchange at 42° to that at 32° (Potonié, 1924, tab. 1, pag. 47). This Q_{10} value holds for the whole range of temperature from 32° up till 42°. So it is much better to estimate Q_{10} for smaller, overlapping ranges of

TABLE 4

Q_{10} of O_2-consumption for some animals, calculated from the tables given by Potonié

Temp. °C	Q_{10}		
	Porcellio scaber		*Deilephila euphorbiae*
	(normal)	(high temp.)	
2,5– 7,5	2.48		
5 –10	2.56		
7,5–12,5	4.00		
10 –15	**5.08**		1.62
12,5–17,5	5.06		1.93
15 –20	4.7		2.35
17,5–22,5	4.0		2.72
20 –25	3.14	2.15	3.38
22,5–27,5	2.53	3.44	**3.50**
25 –30	2.18	4.00	3.15
27,5–32,5	1.75	4.00	3.13
30 –35	1.39	**4.47**	3.22
32,5–37,5		2.98	3.58

temperature, for instance 5° at a time. If one performs this calculations with the figures given by Potonié, one always finds a maximal Q_{10} at those temperatures to which the animals are accustomed (table 4).

Porcellio scaber e.g., which normally prefers much colder habitats than *Deilephila*, has indeed a maximal Q_{10} at a lower temperature. But if *Porcellio* artificially has been accustomed to higher temperatures the maximal Q_{10} is found to be shifted to higher temperatures too (table 4).

So there seems to be a general rule in all these investigations. Only Krüger found on *Ascaris lumbricoides* minimal, irregular Q_{10} values at the temperatures to which this enteroparasite is accustomed, between 37°—40° C. Perhaps we must leave out of account these animals, as they have such an extraordinary metabolism.

Still, it is impossible to explain the appearance of this maximal Q_{10}, which only is the expression of a quickly changing gas-exchange. At any rate it is, probably, not due to an increasing liveliness of the animal for the same is to be found in pupas of *Deilephila*, which only have a much reduced activity.

Summary:

Q_{10} values are calculated for CO_2-output of tench (*Tinca tinca* L.) and *Cichlasoma bimaculatum* (L.).

For normal tench the Q_{10} is maximal at temperatures, between 10° and 17.5°.

By accustoming the animal during several weeks to higher temperatures, the maximal value for Q_{10} is to be found at a higher temperature too.

The gas-exchange of *Cichlasoma bimaculatum* did not show a maximal Q_{10} within physiological range of temperature.

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ZUR BIOLOGIE VON LOLIGO VULGARIS LAM.

VON

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In den Jahren 1932–1940 kaufte die Zoologische Station in Den Helder grosse Mengen Kalmare (*Loligo vulgaris* Lam.) von den dortigen Fischern. Anfangs geschah dies aus faunistischem Interesse, da die Art im Nordseegebiet selten sein sollte (TESCH 1908, GRIMPE 1925). Es zeigte sich sehr bald, dass dies für die Umgebung von Den Helder nicht zutrifft und dass die Tiere hier alljährlich in grosser Anzahl zum Laichgeschäft ins Küstenmeer wandern. VERWEY benutzte diese Gelegenheit die Biologie der Art auch in anderer Hinsicht zu studieren. Seine Beobachtungen bezogen sich insbesondere auf das Wachstum, die Fortpflanzungsverhältnisse und den Zug. Sie umfassten im Ganzen 12000 Stück, deren Grösse, Geschlecht, Entwicklungszustand der Gonaden, Fundort und Funddatum notiert wurden. Die Auswertung dieser Notizen überliess er TINBERGEN. Sie bildet das Thema des vorliegenden Beitrags, der von TINBERGEN, unter Mitarbeit von VERWEY, geschrieben wurde.

Diese Arbeit will nicht mehr sein als eine erste Orientierung, die zufolge der Methode eine gewisse Heterogenität zeigt. Die Wanderungen der Kalmare nehmen in ihr einen wichtigen Platz ein; es ist versucht worden, ihre Behandlung durch vergleichende Betrachtung wertvoller zu machen.

Der Inhalt ist nach folgenden Punkten angeordnet:

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1. WACHSTUM UND ALTER; DIE TEILNAHME DER ALTERSKLASSEN AM ZUGE

Bei unseren weiteren Betrachtungen ist Kenntnis des Wachstums und des Alters öfters unentbehrlich. Wir fangen deshalb mit diesem Abschnitt der Untersuchungen an.

Für die Feststellung des Wachstums benutzten wir vor Allem die Frequenzverteilung der Grössen und zwar der ventralen Mantellängen. Altersmerkmale wie die Schuppen- und Otolithenringe der Fische wurden trotz wiederholter Bemühungen nicht gefunden.

In den Frequenzkurven wurden die gemessenen Längen folgendermassen in Klassen untergebracht: 10.5–11.4 cm wird 11 cm-Klasse, 11.5–12.4 cm wird 12 cm-Klasse u.s.w.

Die Beobachtungszeit ist in 4 Perioden („bis zum 20. V.", „21. V.–20. VI.", „21. VI.–20. VII." und „nach dem 20. VII.") aufgeteilt, welche als solche von je einem Monat aufzufassen sind. Zwar sind in der ersten Periode auch vor dem 21. IV., in der letzten auch nach dem 20. VIII. gemessene Tiere begriffen, doch wurde die Mehrzahl der übrigen Messungen in der zweiten Hälfte der ersten, bzw. in der ersten Hälfte der letzten Periode vorgenommen, so dass die gefundenen Mittelwerte immerhin als Monatsziffern betrachtet werden können.

Zur Beurteilung des Wachstums der Männchen betrachten wir zunächst Abb. 1, in der die Messungen aller Jahre vereint sind. Die Frequenzkurven zeigen folgende Gipfelpunkte:

bis zum 20. V.	13–14 cm	20–22 cm
21. V.–20. VI.	15 cm	23 cm
21. VI.–20. VII.	15–18 cm	23–27 cm
nach dem 20. VII.	17–18 cm	?

Man könnte in diesen Gipfeln zwei Jahresklassen sehen; verfolgt man diese aber in den Kurven der einzelnen Jahre (Abb. 2), so findet man viele Unregelmässigkeiten und daher ein wenig überzeugendes Bild. Es wäre also möglich, dass die Zweigipfligkeit der Abb. 1 rein zufällig entstanden ist und bei einer anderen Zusammenfügung der Jahre verschwinden würde. Dass letzteres jedoch nicht der Fall ist, geht aus Abb. 3 hervor, in der die Kurven für einige solcher Kombinationen eingezeichnet sind. Auch hier treten die zwei Gipfel recht deutlich hervor. Die Unregelmässigkeiten der Kurven der einzelnen Jahre sind also wahrscheinlich auf zu geringen Umfang des Tatsachenmaterials zurückzuführen.

Wir nehmen daher vorläufig an, dass zwei aufeinanderfolgende

Jahresklassen von ♂♂ am Laichzuge teilnehmen. Nach ihrer ventralen Mantellänge in der Periode bis zum 20. V. werden wir sie als „13 cm-Klasse" und „21 cm-Klasse" bezeichnen.

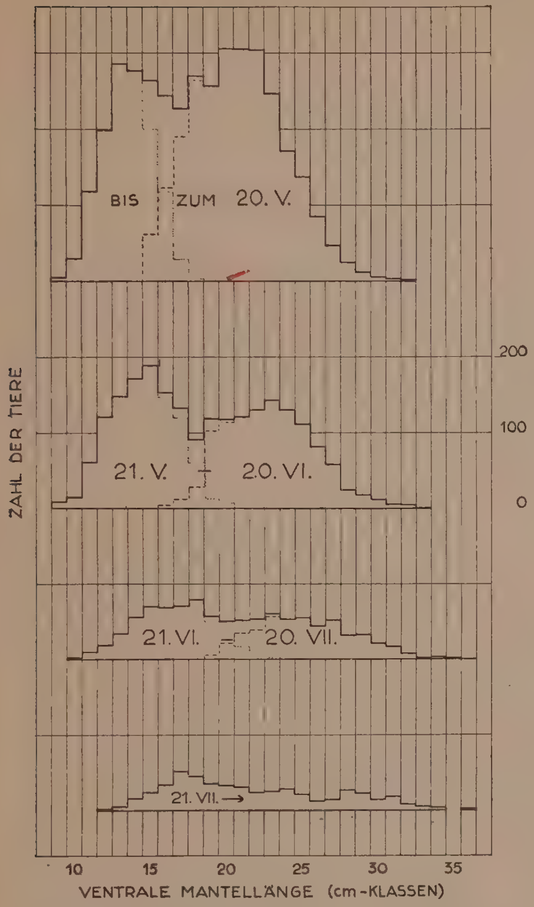

Abb. 1. Längenfrequenzkurven sämtlicher ♂♂. Nicht eingezeichnet: 1 ♂ von 42 cm, 21. V.–20. VI.; 1 ♂ von 39 cm, 21. VII. →.

Inwieweit diese Annahme berechtigt ist, kann uns in erster Linie der Wachstumsverlauf zeigen. Zwischen der ersten und letzten Messungsperiode, d.h. im Durchschnitt etwa vom 5. V. bis zum 5. VIII., beträgt das Wachstum der Tiere der 13 cm-Klasse nach obiger Tabelle 4 cm. Nehmen wir an, dass die Wassertemperatur den Zuwachs bestimmt, so können wir das Wachstum in den nächsten 3 Monaten (nämlich in der Periode 5. VIII.–5. XI.) auf etwas weniger als 4 cm, wir wollen annehmen auf ungefähr $3\frac{1}{2}$ cm, einschätzen. Dabei berücksichtigen wir, dass im Meere das jährliche Temperaturmaximum etwas später als auf dem Lande erreicht wird und in Küstennähe auf Ende Juli, Anfang August zu setzen ist. Die Tiere der 13 cm-Klasse würden also in der Periode 21. X.–20. XI. einen Gipfel bei 21 cm zeigen und müssten – wenn sie tatsächlich mit der 21 cm-Klasse des nächsten Jahres korrespondierten – während der Periode 5. XI.–5. V. nicht wachsen. Durch ihre Abwesenheit im Beobachtungsgebiet sind aus dieser Jahreszeit keine Beobach-

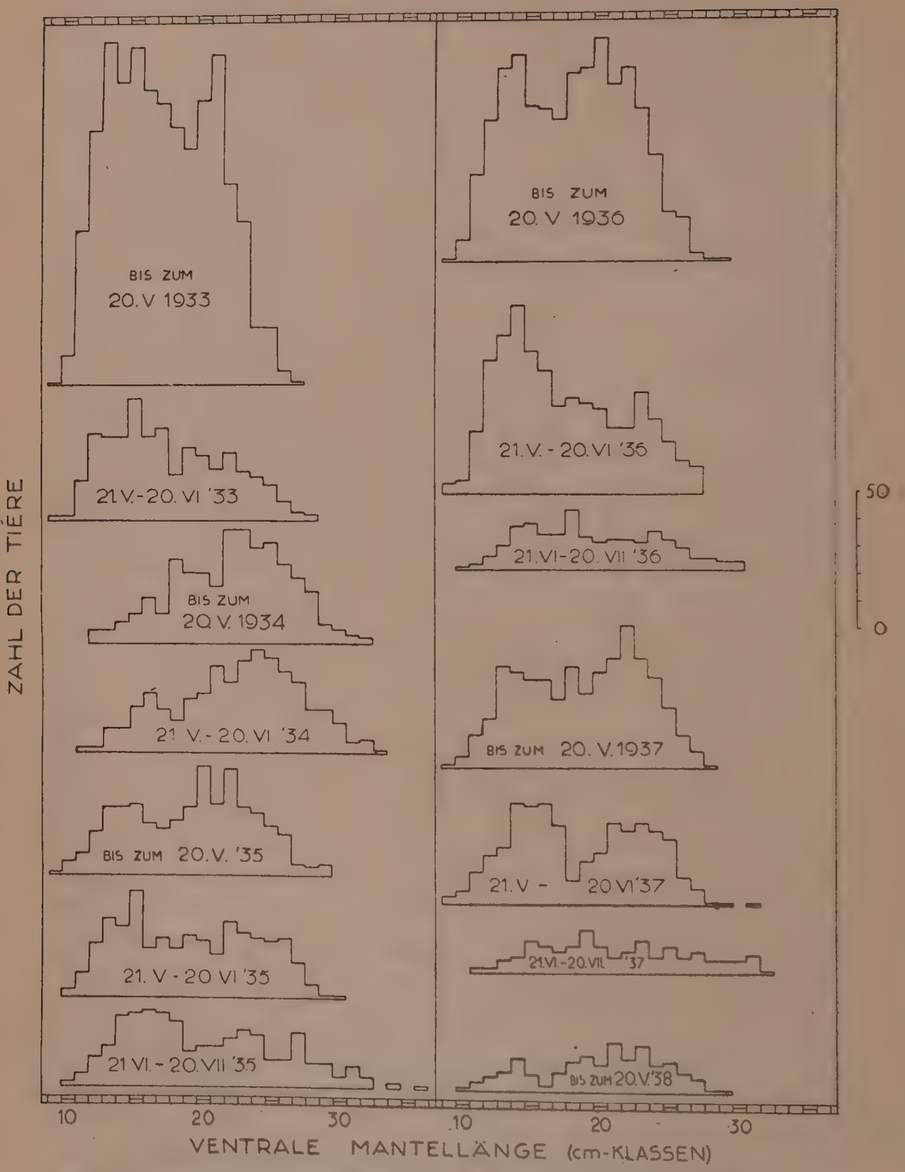

Abb. 2. Längenfrequenzkurven der ♂♂. Daten der einzelnen Jahre. Einige sehr kleine Monatfänge sind nicht eingetragen.

tungen vorhanden; wir besitzen solche aber für die jungen, eben geborenen Tiere und aus diesen geht hervor, dass bei ihnen während der Wintermonate das Wachstum tatsächlich fast still steht. Der Zuwachs der im Sommer geborenen Tiere beträgt nämlich, wie sich weiter unten zeigen wird, vom Juni (Juli) bis Anfang Oktober etwa $8\frac{1}{2}$ cm (Anfangslänge $\frac{1}{2}$ cm), von Anfang Oktober bis Anfang Dezember etwa 3 cm und von Anfang Dezember bis Anfang Mai nur etwa $1\frac{1}{2}$ cm. Diese Überlegungen haben uns deshalb davon überzeugt, dass die 13 cm-Klasse mit der 21 cm-Klasse des nächsten Jahres identisch ist.

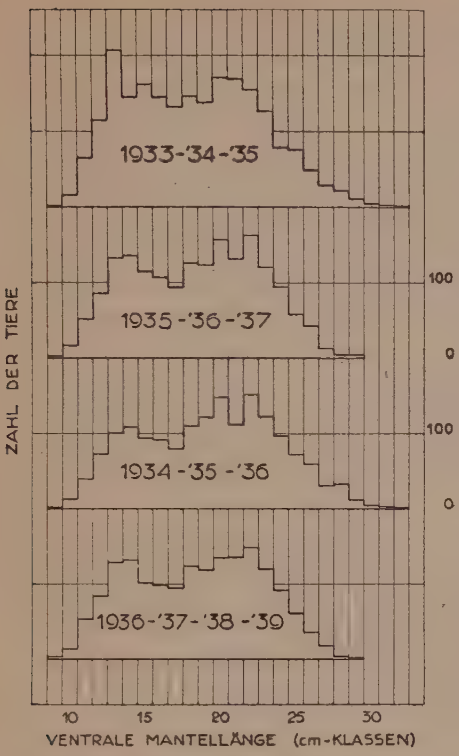

Abb. 3. Längenfreguenzkurven der ♂♂. Periode bis zum 20. V. Kombinationen verschiedener Jahre. Siehe den Text.

Die relative Häufigkeit der beiden Klassen in verschiedenen Jahren könnte auch Hinweise auf ihre gegenseitigen Beziehungen geben. So ist 1933 die 13 cm-Klasse und 1934 die 21 cm-Klasse verhältnismässig häufig, was darauf hindeuten mag, dass die beiden identisch sind. Weitere Argumente für oder gegen unsere Auffassung sind aber aus dem Material kaum abzuleiten.

Es fragt sich nun, wie alt die 13 cm-Klasse ist. Leider stehen uns von den ersten Jugendstadien nur wenige Angaben zur Verfügung. Die im Juni und Juli öfters im Aquarium unsrer Station ausschlüpfenden Kalmare sind etwa 0.5 cm lang. Drei an der belgischen Küste (Ostende) am 4. IX. 1934 gefangene Jungtiere hatten laut freundlicher Mitteilung von Dr. ADAM (1941 in litt.) ventrale Mantellängen von 2.6, 3.5 und 4.0 cm. Bei 6 ♂♂, die zwischen dem 28. IX. und 24. X. 1934 bei Den Helder erbeutet wurden, betrug die ventrale Mantellänge 6.0, 7.9, 9.4, 9.8, 10.3 und 10.4 cm. Schliesslich wurden zwischen dem 24. XI. und dem

18. XII. 1939 19 ♂♂ mit einer mittleren Länge van 12.1 cm und nachfolgender Frequenzverteilung gefangen:

9	10	11	12	13	14	15	16 cm
4	2	2	3	2	2	3	1 Stück

Zur selben Grössenklasse gehört ein von HERTLING (1929) erwähntes ♂ von 12.3 cm, Dez. 1928, beim Feuerschiff Haaks.

Von letzterer Gruppe nun ist es klar, dass sie mit der 13 cm-Klasse des nächsten Frühlings identisch sein muss. Wenn man weiter annimmt, dass diese Tiere etwa ein halbes Jahr alt sind, kann man alle eben erwähnten Stücke in einer fliessenden Wachstumskurve zusammenbringen. Letzteres ist zwar an sich kein Beweis für die Richtigkeit der Annahme, dass die genannten Herbst- und Wintertiere zur 13 cm-Klasse des nächsten Frühlings gehören. Diese Annahme wird aber durch RAJAS (1935) Messungen des postembryonalen Wachstums in starkem Masse unterstützt.

Frl. RAJA gibt viele Gewichte von bei Neapel gefangenen jungen *Loligo vulgaris*. Die Tiere wurden auch gemessen; leider sind die Längen aber nicht erwähnt. Da wir nicht in Verbindung mit Frl. RAJA kommen konnten, waren wir gezwungen die genannten Gewichte mit Hilfe der in Holland gefundenen Verhältniszahl $\frac{\text{ventrale Mantellänge}}{\text{Gewicht}}$ auf Längendaten zurückzuführen. Hierbei kamen wir zum folgenden Ergebnis:

Juli:	ventrale	Mantellänge	1–4	cm,	durchschn.	1 cm
Aug.:	„	„	1–6	cm,	„	3 cm
Sept.:	„	„	1–7	cm,	„	4 cm
Okt., Nov.:	„	„	4–10	cm,	„	7 cm
Dez., Jan.:	„	„	9–16	cm,	„	12½ cm

Das Wachstum ist also fast dasselbe wie das von uns für Den Helder angenommene.

LO BIANCO (1909) gibt eine viel raschere Zunahme, gleichfalls für die Umgebung Neapels, an. Nach diesem Autor würden die im Mai geborenen Tiere im Dezember nämlich schon 20 cm lang sein. Da er seine Beobachtungen aber nur summarisch gibt, ist es nicht möglich, ausfindig zu machen, ob hier vielleicht ein Irrtum vorliegt.

In dieser Beziehung interessieren uns auch die Masse einiger von ADAM (1942, in litt.) untersuchten Jungtiere der afrikanischen Westküste (Pulpito Baie, Villa Cisneros und Angra de Cintra (Rio de Oro)), welche im November 1935 und 1936 gesammelt wurden:

2	3	4	5	6	7 cm
1	4	2	11	12	4 Stück

Genau wie die neapeler Tiere waren diese etwas kleiner als die holländischen Novembertiere; sie waren also entweder langsamer gewachsen oder später geboren.

Abb. 4 gibt eine schematische Übersicht unserer Beobachtungen über das Wachstum der ♂♂. Sie gründet sich auf Abb. 1. Wir haben ja die dort gegebenen Kurven so interpretiert, dass die zwei Gipfel die zwei Jahresklassen andeuten, die beim Laichzuge eine Rolle spielen. Die Frequenzkurven von jeder dieser zwei Jahresklassen sind in Abb. 1 schätzungsweise eingezeichnet unter der Annahme, dass die Verteilung der 13 cm-Klasse symmetrisch sei, was natürlich nicht richtig zu sein braucht, uns für unsre Zwecke aber erlaubt scheint. Die so erhaltenen Einzelkurven sind in Abb. 4 in wiederum vereinfachter Form eingezeichnet worden. Wir bekommen so eine klare Übersicht über das Wachstum bis zur Vollendung des zweiten Lebensjahres. Der Gipfel der etwa 24 Monate alten Tiere liegt nach Abb. 1 bei 24–26 cm; die grössten unter ihnen sind 30 bis 36 cm lang. Einzelne, grössere Tiere gehören wahrscheinlich einer älteren, wohl der dritten Jahresklasse an. Vor Allem scheint uns dies von zwei Stücken der Fall zu sein: ♂ 38.7 cm (21. VII. 1933) und ♂ 42.4 cm (3. VI. 1939).

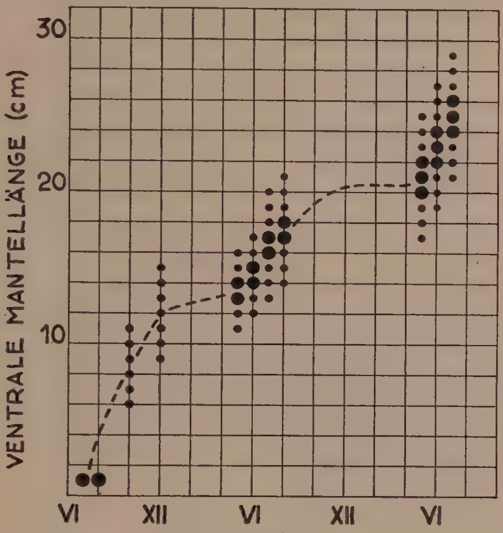

Abb. 4 Schematische Übersicht des Wachstums der ♂♂.

Bei dem Laichzuge spielen also nur zwei Jahresklassen eine wesentliche Rolle.

Es fällt auf, dass die zweijährigen Tiere im Durchschnitt etwas häufiger sind als die einjährigen, während man von einer älteren

Jahresklasse erwarten würde, dass sie durch Sterblichkeit abgenommen hätte. Wir messen aber nur Laichzügler. Anscheinend nimmt von den einjährigen Tieren ein geringerer Prozentsatz am Zuge teil als von den zweijährigen. Das Missverhältnis zwischen ein- und zweijährigen ist am grössten in der Periode bis zum 20. V. Hieraus geht hervor, dass die zweijährigen relativ früher einwandern als die einjährigen.

Das Wachstum der Weibchen scheint von der Geburt bis zum ersten Winter nicht von dem der ♂♂ abzuweichen. So weisen 8 Oktobertiere keinen grossen Unterschied zu den oben beschriebenen ♂♂ aus diesem Monat auf, indem ihre Länge 6.0, 7.3, 7.4, 7.5, 8.0, 8.5, 8.8 und 9.0 cm beträgt. Während 19 im November und Dezember 1939 gefangene ♂♂ im Durchschnitt 12.1 cm messen (S. 218), haben 14 in derselben Zeit gefangene ♀♀ eine durchschnittliche ventrale Mantellänge von 11.7 cm.

Die im Sommerhalbjahr gefundenen Längenfrequenzkurven geben aber ein ganz anderes Bild als diejenigen der ♂♂. In Abb. 5 sehen wir sie als schmale symmetrische Kurven mit folgenden Gipfelpunkten:

bis zum 20. V.	14–15 cm,
21. V.–20. VI.	14–15 cm,
21. VI.–20. VII.	15–16 cm,
nach dem 20. VII.	15–17 cm.

In der ersten Periode liegt der Gipfel etwa 1 cm höher als bei den einjährigen ♂♂; später bleibt er aber ganz zurück.

Man könnte sich nun durch den Anblick der symmetrischen eingipfligen Kurven zu der Folgerung verleiten lassen, dass die ♀♀ nur eine einzige Jahresklasse umfassen. Es wäre aber auch denkbar, dass es mehrere Jahresklassen gäbe, die durch teilweises Zusammenfallen eine gemeinsame „Trug"-kurve bilden. Welche der beiden Lösungen zutrifft, ist aus den Gesamtkurven nicht zu ersehen. Wir brauchen hierzu die Kurven der einzelnen Jahre, welche zum grössten Teil in der Abb. 6 dargestellt sind und deren Gipfel weiter in untenstehender Tabelle zusammengefasst werden.

	1933	1934	1935	1936	1937	
bis zum 20. V.	14–15	17–18	14–15	14–15	14–15	cm
21. V.–20. VI.	13–15	17–19	<15	14	14	cm
21. VI.–20. VII.	16	16–19	15–16	15	16	cm
nach dem 20. VII.	17	?	16	15–16	17	cm

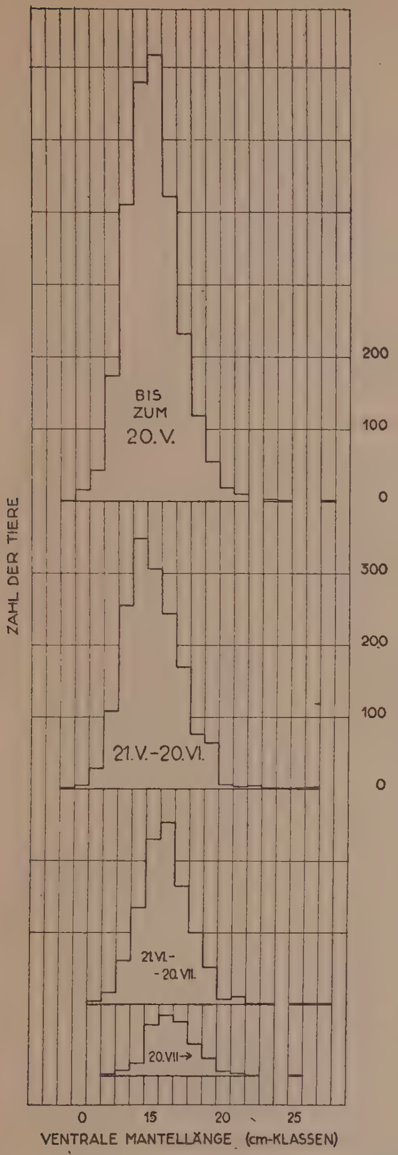

Abb. 5. Längenfrequenzkurven sämtlicher ♀♀.

Die Gipfel liegen in den verschiedenen Jahren bei etwa derselben Mantellänge; nur im Jahre 1934 sind sie erheblich nach rechts verschoben. Gesetzt der Fall, es handelte sich bei den ♀♀ nur um eine einzige Jahresklasse, so müsste das Wachstum im Nachsommer 1933 oder im Winter 1933–'34 etwa 20% stärker als gewöhnlich gewesen sein. Wenn wir jetzt die Diagramme der ♂♂ zum Vergleich heranziehen, zeigt es sich, dass bei den Tieren dieses Geschlechtes im Jahre 1934 die Gipfel bedeutend weniger als 20% und zwar für die einjährigen etwa 10% und für die zweijährigen 5% über den durchschnittlichen liegen. Man findet nämlich:

		Einjährige:	Zweijährige:
bis zum 20. V.	1934	16??	22–23 cm
	durchschn.	13–14	21 cm
21. V.–20. VI.	1934	16	23–25 cm
	durchschn.	14–15	22–24 cm

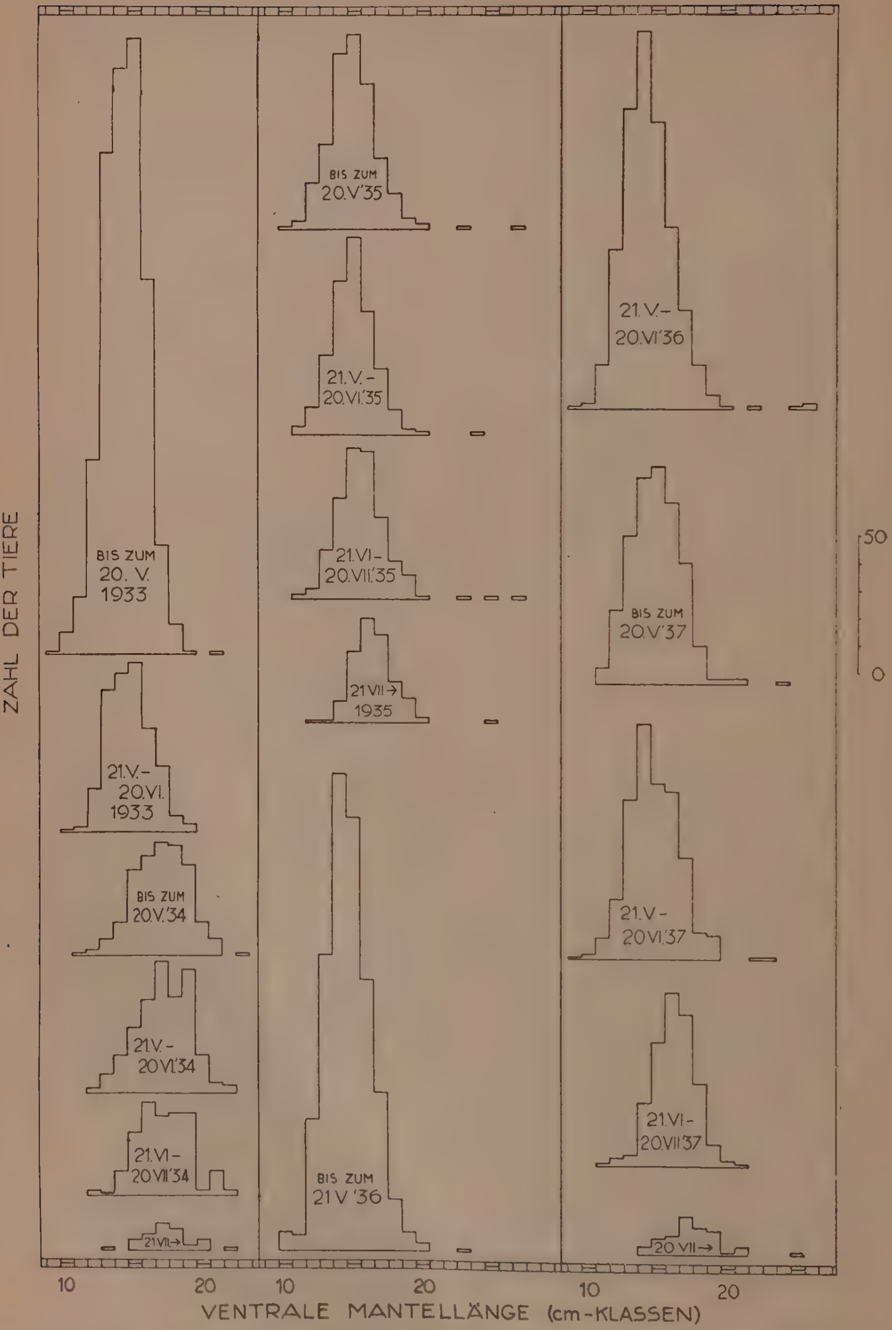

Abb. 6. Längenfrequenzkurven der ♀♀. Daten der einzelnen Jahre. Einige sehr kleine Monatfänge sind nicht eingetragen.

Deshalb ist es nicht wahrscheinlich, dass die abweichende Lage des Weibchengipfels im Jahre 1934 nur vom starken Wachstum im Jahre 1933 hervorgerufen wurde. Wir sahen schon S. 217, dass 1934 die einjährigen ♂♂ verhältnismässig sehr wenig häufig waren, woraus wir vielleicht folgern dürfen, dass die Brut 1933 schlecht gelang. Es ist nicht wahrscheinlich, dass letzteres nur für die ♂♂ und nicht auch für die ♀♀ gelten würde. Die im Jahre 1934 gefundenen abnorm grossen Längenwerte der ♀♀ müssen denn auch nach unsrer Ansicht so gedeutet werden, dass nicht nur die Tiere im vorangehenden Jahre schnell gewachsen sind, sondern auch der Prozentsatz der einjährigen Tiere abnorm klein war.

Schlechtes Gelingen der Brut und gutes Wachstum der Tiere sind, im Allgemeinen, nicht unvereinbar, da das Gelingen der Brut von anderen Faktoren abhängig sein kann als das Wachstum der jungen Tiere. So könnte der extrem warme Herbst 1933 das Wachstum stark gefördert haben, während er ohne Einfluss auf das Gelingen der Brut blieb.

Wir nehmen also an, dass die ♀♀, wie die ♂♂, aus Tieren von zwei Jahresklassen bestehen, deren Längenfrequenzkurven zusammen ein eingipfliges Diagramm bilden. Die Lage der Gipfel der einzelnen Jahresklassen im Monat Mai schätzen wir für die einjährigen auf 13–14 cm und für die zweijährigen auf 17 cm. Ersteren Wert haben wir gewählt, weil die Tiere nach S. 220 in ihrem Geburtsjahre etwa gleich schnell wie die ♂♂ wachsen, deren Gipfel ja den genannten Wert hat. Letzterer Wert beruht auf den Beobachtungen des Jahres 1934. Wir nehmen nämlich an, dass in diesem Jahre der beobachtete Gipfel (17–18 cm), dank der geringen Zahl der einjährigen, sich nicht viel von dem der zweijährigen unterscheidet. Wir zeigten aber ausserdem, dass die Längenwerte der zweijährigen ♂♂ im Jahre 1934 etwa 5% höher als im Durchschnittsjahr lagen. Deshalb schätzen wir den normalen Gipfel der zweijährigen ♀♀ auf ungefähr 17 cm.

Nach dieser Auffassung würde das Wachstum der ♀♀ vom Monat Mai am Ende des ersten bis zum Mai am Ende des zweiten Lebensjahres rund 3 cm betragen, d.h. noch nicht die Hälfte der entsprechenden Längenzunahme der ♂♂, die wir (vgl. S. 215) auf 7–8 cm veranschlagen können. Das stimmt gut zu den direkten Beobachtungen des Wachstums während der Sommermonate. Denn die Längen der einjährigen ♂♂ nehmen während der Periode 5. V.–5. VIII. um 4 cm zu (Abb. 1) und diejenigen sämtlicher ♀♀ nur um kaum 2 cm (Abb. 5). Es ist also klar, dass die einjährigen ♀♀ während der Periode 5. V.–5. VIII. weniger als 2 cm zunehmen, d.h., wie bei der obigen Schätzung der jährlichen Längenzunahme, weniger als die Hälfte des Zuwachses der ♂♂. Die Sommerbeobachtungen unterstützen also die Annahme des Bestehens zweier Jahresklassen bei den ♀♀. Trotz der grossen Unterschiede in den Frequenzkurven der ♂♂ und ♀♀ müssen wir also annehmen, dass auch unter den ♀♀ ein und zwei Jahre alte Tiere vorkommen.

Vielleicht findet man auch Weibchen höheren Alters. Es gibt einzelne, 23–27 cm messende Stücke, von denen man nicht feststellen kann, ob sie sehr stark ausgewachsene zweijährige oder normale dreijährige Tiere sind (vgl. Abb. 6). Wir nehmen inzwischen an, dass letzteres zutrifft.

Schliesslich muss hervorgehoben werden, dass die grösseren ♀♀, wie die älteren ♂♂, etwas früher als die kleineren ins Küstengebiet kommen. Denn im Durchschnitt nimmt die Länge der ♀♀ zwischen dem 1. und 2. Beobachtungsmonat (Abb. 5) etwas ab, während man Zunahme oder höchstens Stillstand erwarten würde, wenn die Population von unveränderlicher Zusammensetzung wäre. Es findet also eine relative Zunahme der Anzahl der jüngeren Tiere statt.

Betrachten wir jetzt nochmals einige unsrer Ergebnisse. Wie wir sahen, erreichen die ♂♂ nach einem Jahr eine durchschnittliche Länge von 13–14 cm und ein Jahr später von 21 cm. Bei den ♀♀ betragen diese Zahlen etwa 13–14 cm und ungefähr 17 cm. Nach ihrem ersten Jahre wachsen die ♀♀ also bedeutend langsamer als die ♂♂. Es liegt auf der Hand, hier Zusammenhang mit der grossen Energie zu suchen, welche die Eierproduktion bei den ♀♀ fordert. Letztere fängt bei unsrer Art zwischen Dezember und April des ersten Lebensjahres an.

Über das Wachstum von *Loligo vulgaris* in anderen Gebieten ist leider nicht so viel bekannt, dass wir hier Vergleichungen anstellen können. Auch von verhältnismässig wenigen anderen Cephalopodenarten liegen zuverlässige Daten vor.

Die amerikanische *Loligo pealii* Les. wächst ungefähr gleich schnell wie *Loligo vulgaris*. Auch hier hat das ♀ nach dem ersten Lebensjahre ein langsameres Wachstum als das ♂. VERRILL (1882) gibt an, dass im Juni geborene Stücke dieser Art im November eine ventrale Mantellänge von 8 cm erreichen. Im Mai und Juni des nächsten Jahres schwanken die Längen der einjährigen zwischen 6 und 18 cm, die der zweijährigen ♂♂ zwischen 20 und 27.5 cm, die der zweijährigen ♀♀ zwischen 17.5 und 22.5 cm. Ältere Tiere kommen wenig vor; auch hierin ähnelt die Art der unsrigen.

Dagegen erreicht *Sepia officinalis* L. an der holländischen Küste ein höheres Alter. Tiere von 3 Jahren sind nach unserer Feststellung ziemlich häufig; wahrscheinlich kommen noch ältere vor. Wie bei *Loligo vulgaris* wachsen die ♀♀ von *Sepia officinalis* in ihrem zweiten Lebensjahre langsamer als die ♂♂.

Sowohl die ♂♂ wie die ♀♀ von *Loligo vulgaris* ziehen im zweiten Lebensjahr früher ins Küstenmeer hinein als im ersten. Solch eine Reihenfolge der Altersklassen ist bei vielen zum Fortpflanzungsgebiet wandernden Tieren festgestellt worden.

Einige Beispiele folgen hier; auf Vollständigkeit müssen wir aber verzichten. Ein früherer Zug der älteren Tiere ist unter den Cephalopoden bei *Sepia officinalis* L. festgestellt worden (eigene Beobachtungen), unter den Fischen bei *Clupea harengus* L.[1]), *Oncorhynchus tschwawytscha* (Walbaum), *Salmo salar* L., *Salmo trutta* L., *Fundulus heteroclitus* (L.), *Pleurogrammus monopterygius* (Pallas), *Merluccius vulgaris* Flem., (SCHEURING 1929–'30) und unter den Vögeln „vielfach bei grösseren Arten'' (STRESEMANN 1927–'34) [So bei *Ardea cinerea* L. (VERWEY 1930), *Ciconia ciconia* L. (SCHÜZ 1940), *Phalacrocorax carbo sinensis* (Shaw & Nodder) (KORTLANDT 1942)], weiter bei *Sturnus vulgaris* L. (KLUYVER 1935, VAN DOBBEN und MÖRZER BRUYNS 1939), *Melospiza melodia* (Wilson) (NICE 1937). Die umgekehrte Reihenfolge scheint beim Hecht (*Esox lucius* L.) vorzukommen (SCHEURING 1929-'30). Keinen Unterschied im Erscheinungsdatum zeigen die verschiedenen Altersklassen der Feldlerche *Alauda arvensis* L. (VAN DOBBEN und MÖRZER BRUYNS 1939).

Bei der Mehrzahl dieser Arten scheinen also wie bei *Loligo vulgaris* die älteren Tiere früher als die jüngeren ins Laichgebiet zu wandern.

Bei Vögeln vollzieht sich die geschlechtliche Reifung öfters gleichartig. Für die schon erwähnten Arten *Sturnus vulgaris* und *Melospiza melodia* haben z.B. KLUYVER (1935) und NICE (1937) festgestellt, dass die Gelege einjähriger ♀♀ durchschnittlich später als die der überjährigen erscheinen. Hierin äussert sich der enge Zusammenhang zwischen Zugtrieb und Reife, der frühere Autoren zu der Annahme verführt hat, die Reife sei die Ursache des Erwachens des Zugtriebes (vgl. S. 247).

Nach diesem Zustand bei den Vögeln zu urteilen, könnte man erwarten, dass auch bei *Loligo vulgaris* die einjährigen Tiere später reifen als die überjährigen. Dies konnte nicht festgestellt werden, weil während der Reifungszeit zu wenige Stücke erbeutet wurden (vgl. Abschnitt 3). Bei *Sepia officinalis* ist dieses nach unseren Beobachtungen tatsächlich der Fall.

2. DAS GESCHLECHTSVERHÄLTNIS UND DIE REIHENFOLGE DER GESCHLECHTER AUF DEM ZUGE

Insgesamt wurden 7484 ♂♂ und 5657 ♀♀ empfangen, d.h. 57.0% ♂♂ oder 132 ♂♂ auf je 100 ♀♀. In den einzelnen Jahren kann das Geschlechtsverhältnis beträchtliche Schwankungen aufweisen. So wurden 1933 58% ♂♂ erbeutet; 1934 61%; 1935 60%; 1936 53% und 1937 53%. In jedem dieser Jahre wurden mehr als 1500 Tiere untersucht.

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[1]) Nach HODGSON (1934) soll jedoch in der südlichen Nordsee die umgekehrte Reihenfolge auftreten.

Der Wert dieser Zahlen ist recht ungewiss. Es besteht z.B. die Möglichkeit, dass die ♂♂ sich leichter fangen lassen als die ♀♀. Ausserdem ist die Interpretierung der Ergebnisse bei einer wandernden Art wie der unsrigen nicht einfach. Das ungleiche Geschlechtsverhältnis könnte nämlich auf einer grösseren Zahl der ziehenden ♂♂, auch aber auf einer längeren Verbleibszeit pro ♂ Individuum beruhen. Schliesslich muss man damit rechnen, dass man nur über das Geschlechtsverhältnis der am Laichzuge ins holländische Küstengebiet teilnehmenden Tiere Schlüsse ziehen kann und dass diese Schlüsse sich nicht ohne Weiteres für die ganze Art verallgemeinern lassen.

Weniger gefährlich ist die Deutung der Änderung des Geschlechtsverhältnisses im Laufe jedes Jahres. Aus dieser ist die Reihenfolge im Auftreten der Geschlechter auf dem Zuge abzuleiten; letztere ist schon bei sehr verschiedenen Wandertieren bekannt und gibt Anlass zu Vergleichungen.

Abb. 7 gibt die diesbezüglichen Zahlen im Gesamtergebnis. Es ist klar, dass ♂♂ und ♀♀ fast zu gleicher Zeit im Küstengebiet eintreffen, die ♀♀ aber im Durchschnitt bis etwas später im Jahr zur Beobachtung kommen als die ♂♂. Bei genauer Betrachtung der Fangzahlen erhält man jedoch den Eindruck, dass die ♂♂ verhältnismässig etwas früher als die ♀♀ ankommen, denn ihre relative Häufigkeit nimmt allmählich ab und beträgt im April 61%, im Mai 58%, im Juni 53% und im Juli–August 53%. Betrachtet man die Fänge aus der ersten Woche des April, in der die Tiere häufig sind, gesondert, so findet man eine noch etwas gesteigerte ♂♂-Zahl, nämlich 62%. All diese Zahlen scheinen ziemlich eindeutig; vergleicht man aber das Ergebnis in den einzelnen Jahren, so scheint diese Reihenfolge der Ge-

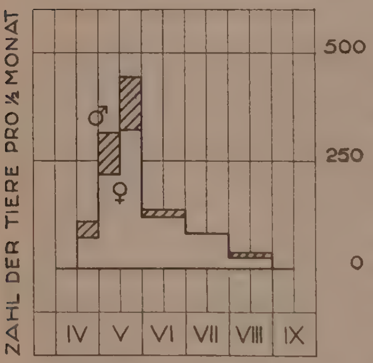

Abb. 7. Vorkommen von ♂♂ und ♀♀. Durchschnittswerte 1932–1940. Zahlen für ♂♂ und ♀♀ von der Basislinie zu rechnen.

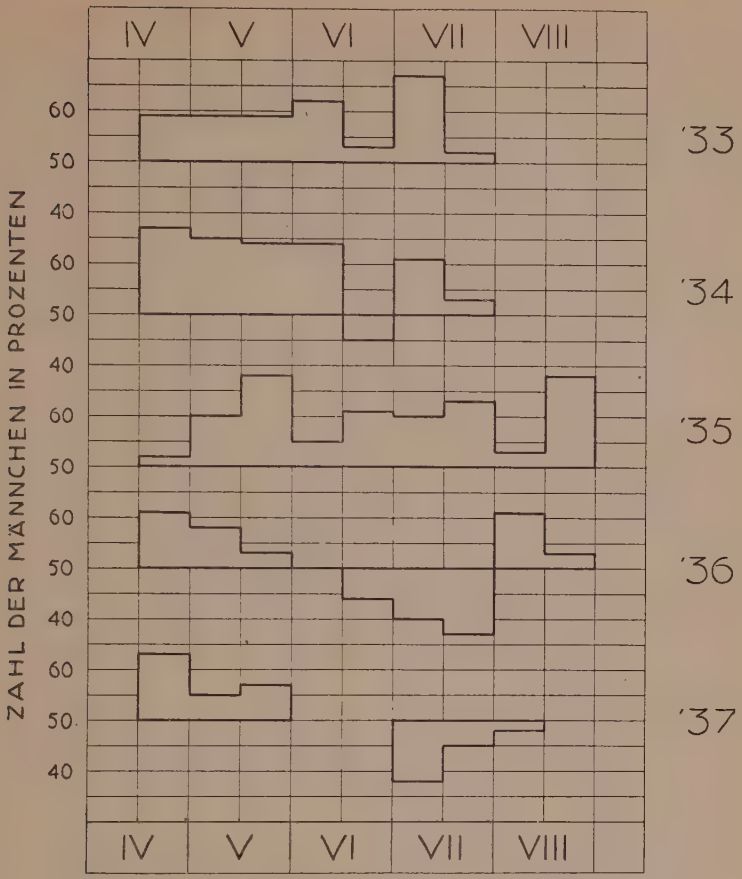

Abb. 8. Geschlechtsverhältnis in den einzelnen Jahren.

schlechter doch nicht jedes Jahr vorzukommen. Abb. 8 stellt die diesbezüglichen Daten dar. In den Jahren 1933 und 1934 kommen die beiden Geschlechter etwa zu gleicher Zeit an; 1935 erscheinen die ♀♀ relativ früher, 1936 und 1937 schliesslich die ♂♂.

Wir werden dieses Ergebnis mit einigen Literaturdaten von anderen Tierarten vergleichen.

Am besten sind wir über diese Verhältnisse bei den Vögeln unterrichtet. Tabelle 1 zeigt verschiedene Beispiele. Anscheinend sind die drei denkbaren Möglichkeiten (♂♂ vor ♀♀; ♀♀ vor ♂♂; ♂♂ und ♀♀ zu gleicher Zeit) alle erfüllt. Für uns ist es weiter von Interesse, dass die Reihenfolge der Geschlechter bei den Vögeln Zusammenhänge mit der Paarungsbiologie aufweist. Deshalb sind auch Angaben über diese in der Tabelle aufgenommen worden. Wir kommen nun zu folgenden Regeln:

Bei Arten, die sich im Wintergebiet paaren, bzw. eine Ehe fürs Leben schliessen, erscheinen die beiden Geschlechter zu gleicher Zeit im Brutgebiet. Dagegen zeigen die Arten, welche sich erst im Brutgebiet paaren, ein wechselndes Verhalten. Ihr Benehmen hängt von der Paarbildungsweise ab. Zur Beschreibung der Unterschiede lässt sich am besten die von MAKKINK (1942) entworfene Einteilung in „territoriogame" und „soziogame" Arten anwenden. MAKKINK spricht von Territoriogamie, wenn sich die Paarbildung mittels der Revierbesetzung vollzieht und von Soziogamie, wenn sie im Trupp und vor der Revierbesetzung stattfindet. Die Territoriogamie verläuft nach folgendem Schema. Eines der Geschlechter (bei den meisten Arten das männliche) besetzt eine eng begrenzte Stelle und führt hier Balzhandlungen aus, deren Funktion die Abstossung der Geschlechtsgenossen und die Heranlokkung der Tiere des anderen Geschlechtes ist. Letztere streifen umher und binden sich erst bei der Paarbildung an einen bestimmten Ort. Dieses „Territoriumsystem" ist bei den Vögeln (und auch bei anderen Tiergruppen) weit verbreitet. Es wurde von B. ALTUM entdeckt und von H. E. HOWARD zum ersten Male einer ausführlichen Diskussion unterworfen; für weitere Einzelheiten müssen wir auf die diesbezügliche Vogelliteratur hinweisen.

Bei den territoriogamen Arten zieht nun als Regel das revierbesetzende Geschlecht früher im Jahre zum Sommergebiet als das andere. Eine Ausnahme bildet der Kiebitz, der bestimmt territoriogam ist, bei dem aber nach RINKEL (1940) die beiden Geschlechter zur gleichen Zeit ziehen. Trotzdem erscheint nach demselben Autor das revierbesetzende Geschlecht (das ♂) etwas früher im Brutbiotop, so dass sich die Analogie mit den übrigen Arten wieder zeigt.

Wie schon gesagt wird die Rolle des Revierbesetzers bei den meisten territoriogamen Arten vom ♂ gespielt. Es gibt nur einzelne Arten, bei denen sie vom ♀ erfüllt wird. Bei dem einzigen dokumentierten Beispiele (*Phalaropus lobatus*) erscheinen auch tatsächlich die ♀♀ früher im Brutgebiet (sieh Tabelle 1).

Die soziogamen Arten sind im Gegensatz zum Obigen nach aller Wahrscheinlichkeit dadurch gekennzeichnet, dass die beiden Geschlechter zur gleichen Zeit erscheinen. Allerdings ist uns dieses nur von zwei Beispielen (*Charadrius hiaticula* und *Larus argentatus*) bekannt. Andere Arten sind nicht untersucht worden (Es sei hinzugefügt, dass *Larus argentatus* zwar kein charakteristischer Zugvogel ist, jedoch im Frühling eine bestimmte Entfernung vom Nahrungsgebiet zum Brutgebiet zurückzulegen hat).

So scheint bei den Vögeln die Trennung der Geschlechter auf dem Frühlingszuge mit der Territoriogamie verknüpft zu sein. Der Zusammenhang ist so eng, dass man annehmen muss, dass das frühere Erscheinen des revierbesetzenden Geschlechtes notwendig oder wenigsten für die betreffenden Arten vorteilhaft ist.

HOWARD (1920, S. 43) sucht die biologische Bedeutung der Erscheinung hierin, dass die später kommenden ♀♀ einen gleichmässig verbreiteten Männchenbestand antreffen. In welcher Weise dies den Erfolg der Fortpflanzung fördern könnte, erklärt er aber nicht. HOWARDS Deutung kommt uns nicht zwingend vor. Wir sind aber nicht imstande, sie durch eine befriedigendere zu ersetzen und können deshalb nur die Folgerung machen,

TABELLE I

Die Reihenfolge der Geschlechter auf dem Frühlingszuge verschiedener Vogelarten, mit Angaben über die Paarbildung.

N.B. Das Symbol hinter „territoriogam" gibt das Geschlecht des Revierbesetzers an.

Art	Literatur zur Reihenfolge	Paarbildung	Literatur zur Paarbildung
A. ♂♂ vor ♀♀:			
Sturnus vulgaris L.	Hicks (bei Kluyver 1935), van Dobben und Mörzer Bruyns 1939	territoriogam ♂	Kluyver 1933
Fringilla coelebs L.	Hammer 1928	territoriogam ♂	Howard 1920
Melospiza melodia (Wilson)	Nice 1937	territoriogam ♂	Nice 1937
Plectrophenax nivalis (L.)	N. Tinbergen 1939	territoriogam ♂	N. Tinbergen 1939
Alauda arvensis L.	Saxtorph 1928, van Dobben und Mörzer Bruyns 1939	territoriogam ♂	Howard 1920
Sylvidae	Howard 1920	territoriogam ♂	Howard 1920
Ardea cinerea L.	Verwey 1930	territoriogam ♂	Verwey 1930
B. ♀♀ vor ♂♂:			
Phalaropus lobatus	N. Tinbergen 1935	territoriogam ♀	N. Tinbergen 1935
C. ♂♂ und ♀♀ zu gleicher Zeit:			
Anser anser (L.)	Niethammer 1937–'38	Paarung fürs Leben	Heinroth 1911
Anas platyrhyncha (L.)	Niethammer 1937–'38	Paarung im Wintergebiet	Heinroth 1911
Anas querquedula L.	Niethammer 1937–'38	Paarung im Wintergebiet	Heinroth 1911
Charadrius hiaticula L.	Laven 1940	soziogam	Laven 1940
Larus argentatus Pont.	N. Tinbergen mündl.	soziogam	N. Tinbergen 1932

dass es noch unklar ist, welche Bedeutung das frühere Erscheinen des territoriumbesetzenden Geschlechtes hat.

Die Erscheinung der festen Reihenfolge kann zwei Ursachen haben: entweder fangen die beiden Geschlechter zur selben Zeit den Frühlingszug an, doch wandern ungleich schnell, oder aber das zuerst erscheinende Geschlecht verlässt das Überwinterungsgebiet eher. Wir können in dieser Beziehung nur sagen, dass bei *Sturnus vulgaris* wahrscheinlich letztere Möglichkeit zutrifft, da sich die Reihenfolge schon in geringer Entfernung vom Wintergebiete feststellen lässt. Hier scheinen also die Geschlechter ungleiche Schwellen für die zugauslösenden Reize zu haben.

In der Gruppe der Säugetiere finden wir einige Arten, die, wie die Zugvögel, alljährlich zu ihrem Fortpflanzungsgebiet wandern. In Hilzheimers Zusammenstellung (1929) lesen wir, dass diese Wanderungen bei dem See-Elefanten (*Mirounga leonina* (L.)), dem Seelöwen (*Eumetopias* spec.) und dem Seebären (*Arctocephalus ursinus* (L.)) von den ♂♂ frühzeitiger ausgeführt werden als von den ♀♀. In dieser Beziehung interessieren die gleichfalls von Hilzheimer (1914, 1929) zitierten biologischen Darstellungen dieser Arten. Die ♂♂ des See-Elefanten und des Seebären (vom Seelöwen werden keine Einzelheiten gegeben) besetzen am Anfang der Fortpflanzungszeit bestimmte Stellen am Strande, deren Besitz sie sich streitig machen und an denen sie die Weibchenscharen erwarten. Wenn auch ihr Verhalten nicht in jeder Hinsicht mit dem der obenbeschriebenen Vögel übereinstimmt, so scheint uns doch die Analogie mit dem Territoriumsystem so weitgehend zu sein, dass wir es wagen, auch bei diesen Seesäugetieren von Territoriogamie zu sprechen. Wie bei den Vögeln sehen wir also auch hier, dass die zeitliche Trennung der Geschlechter auf dem Laichzuge mit der Territoriogamie verknüpft ist.

Bei Fledermäusen ziehen die ♀♀ am Ende der Winterzeit etwas früher als die ♂♂ zum Sommergebiet, wo sie bald ihre Jungen werfen (Eisentraut 1937). Hier liegen also ganz andere Verhältnisse vor, was aber damit zusammenhängen mag, dass sich die Tiere nicht nach der Ankunft im Sommergebiet begatten, sondern schon im vorhergehenden Herbst gepaart gaben. Bei keinem der bis jetzt behandelten Arten kam Ähnliches vor.

Auch bei den Fischen ziehen die Geschlechter öfters zeitlich getrennt zum Laichgebiet. Zum Beispiel entnehmen wir der Zusammenfassung Scheurings (1929, 1930):

♂♂ vor ♀♀	♀♀ vor ♂♂	♂♂ und ♀♀ zu gleicher Zeit
Clupea harengus L.	*Callionymus lyra* L.	*Oncorhynchus gorbuscha* (Walbaum)
Alosa vulgaris (L.)		*Oncorhynchus keta* (Walbaum)
Oncorhynchus nerka (Walbaum)		
Fundulus heteroclitus (L.)		
Pleurogrammus monopterygius (Pallas)		
Alosa sapidissima (Wilson)		

Salmo salar scheint sich in den verschiedenen Teilen seines Verbreitungsgebietes ungleich zu verhalten. Zusammenhänge mit der Paarungsbiologie sind uns bei den Fischen nicht bekannt.

Wenn wir nach all diesen Ausführungen zu den Cephalopoden zurückkehren, müssen wir in erster Linie feststellen, dass *Sepia officinalis* sich anders als *Loligo vulgaris* benimmt. Bei Sepia erscheinen die ♂♂ im Durchschnitt deutlich früher als die ♀♀, so dass sie in den ersten 2 Wochen ihres Eintreffens 73% gegen im nächsten Monat nur 58% des Gesamtfanges bilden. Es fragt sich deshalb, ob hier auch Unterschiede bei der Paarbildung nachgewiesen werden können. Letztere kennen wir bei *Sepia* durch Aquariumbeobachtungen (L. Tinbergen 1939). Die Art zeigt eine gewisse Übereinkunft mit den territoriogamen Vogelarten. So haben die ♂♂ die Gewohnheit, sich vor der Paarbildung – ohne dass die ♀♀ anwesend sind – zu bekämpfen. Ein Revier nehmen sie im Aquarium nicht ein; ob dieses im Freien stattfindet, ist nicht bekannt. Von *Loligo vulgaris* ist nun leider die Fortpflanzungsethologie ganz unbekannt. Gerade zum Vergleich mit den oben beschriebenen Zusammenhängen wären Einzelheiten über unsre Art höchst wilkommen, zumal es bekannt ist, dass sie vielmehr in Trupps lebt als *Sepia*. So wissen wir heute nur, dass Einbeziehung dieser Gesichtspunkte bei einer künftigen Bearbeitung der Fortpflanzung von *Loligo vulgaris* lohnend sein muss.

3. DER ZYKLUS DER GONADEN UND SEINE BEZIEHUNGEN ZUM ZUGE

Die regelmässigen Beobachtungen über den Gonadenzustand sind in zweierlei Hinsicht von Interesse. Erstens ist der jährliche Zyklus der Geschlechtsorgane bei Cephalopoden wenig bekannt. Zweitens können diese Beobachtungen uns lehren inwieweit Fortpflanzung und Zugverhalten zusammenhängen. Solch ein Zusammenhang besteht bei vielen Wandertieren.

Zuerst geben wir die Beobachtungen über den Gonadenzyklus der Männchen. Die hierbei beschriebenen Stadien sind in Abb. 9 schematisch dargestellt.

Die oben besprochenen Jungtiere vom Oktober und Dezember (S. 217) waren schon erstaunlich weit entwickelt. 6 ♂♂ vom 24. X. 1934 hatten einen schwach geschwollenen Hoden, der bei mikroskopischer Untersuchung eine grosse Menge Spermatozoen aufwies. Das Spermatophorenorgan (Benennung nach Drew 1919) und der Spermatophorensack waren makroskopisch sichtbar, enthielten aber noch keine Spermatophoren. Bei 19 ♂♂, die zwischen dem 24. XI. und 18. XII. 1939 gesammelt wurden, war die Entwicklung bedeutend weiter vorgeschritten. Ihre Hoden waren fast so stark geschwollen wie die der Laichzügler im Frühling. In Ausstrichen konnten Spermatozoen in grosser Menge festgestellt werden. Bei 14 dieser Tiere enthielt der Spermatophorensack sogar schon eine geringe Anzahl allerdings kleiner Spermatophoren; bei den 5 anderen war er leer.

Obgleich wir im Frühwinter also nur Jungtiere mit reifenden Gonaden erhielten, können nicht alle Stücke im Herbste ihres Geburtsjahres so weit entwickelt sein, denn sogar im nächsten

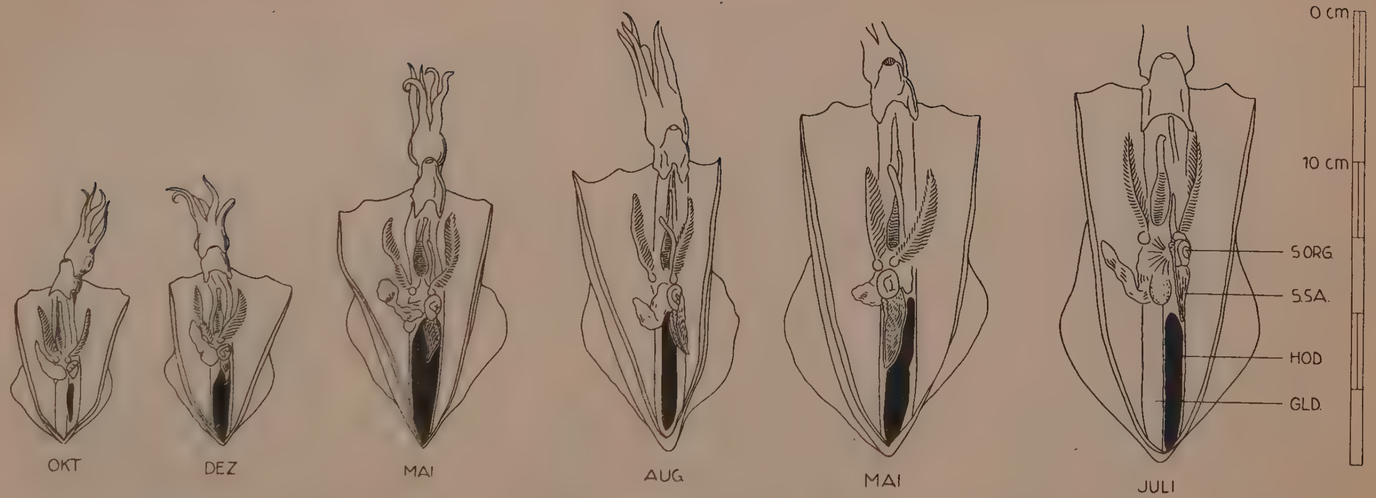

Abb. 9. Gonadenzyklus der ♂♂ von Oktober des Geburtsjahres bis zum Ende des 2. Lebensjahres. Gld. = Gladius, Hod. = Hoden, S. org. = Spermatophorenorgan, S. sa. = Spermatophorensack. Füllungsgrad der Spermatophorensäcke: Mai (1. Jahr) „voll", Aug. (1. Jahr) „halbvoll", Mai (2. Jahr) „voll", Juli (2. Jahr) „viertelvoll".

Sommer kommen noch ganz unreife einjährige Tiere vor, wie wir weiter unten sehen werden.

Aus den Monaten Januar bis März haben wir nur ganz vereinzelte Stücke. Ihr Zustand weist darauf hin, dass sich die Gonaden den ganzen Winter hindurch allmählich weiter entwickeln, oder wenigstens, dass ihre Entwicklung nicht zurückgeht:

21. I. 1937 ♂ 12.0 cm, Hoden ganz entwickelt (5.3 × 1.3 cm). Spermatophorensack enthält eine kleine Anzahl Spermatophoren.

12. III. 1936 ♂ 9.0 cm, Hoden ganz entwickelt, Spermatophorensack wie oben.

13. III. 1936 ♂ 7.6 cm, unentwickelt, Hoden unfindbar, keine Spermatophoren, Hektokotylus deutlich.

Wenn im April die ¾ Jahre alten Tiere in grosser Menge im Küstengebiet erscheinen, haben sie fast alle einen stark geschwollenen Hoden, der auch im Verhältnis zur Länge der Tiere grösser ist als im vorigen Herbst. In Ausstreichpräparaten findet man grosse Mengen Spermatozoen.

Im Laufe des Sommers zeigen fast alle einjährigen Tiere einen stark entwickelten Hoden. Nur bei einem verschwindend kleinen Teil ist das Organ unentwickelt. So kamen neben 4511 reifen ♂♂, die in den Monaten April bis August untersucht wurden, nur 16 „unreife" Stücke vor.

Bei 3 dieser Tiere war der Hoden unfindbar, bei 10 kaum sichtbar und bei 2 weiteren etwas grösser, aber doch wenig geschwollen (bei einem Tier von 13.5 cm z.B. 2.3 × 0.3 cm, d.h. etwa gleich gross wie bei einem Jungtier von 6–9 cm). 15 dieser 16 Tiere wurden im Juli und August gesammelt; sie waren also bedeutend später als ihre reifen Altersgenossen. Ihre ventrale Mantellänge schwankte zwischen 10.1 und 16.0 cm und betrug im Durchschnitt 12.6 cm, d.h. beträchtlich weniger als die der übrigen Einjährigen, die nach S. 214 um diese Zeit 15–18 cm ist. Es handelte sich also um spätgeborene oder im Körperwachstum zurückgebliebene Exemplare.

Wir sahen oben, dass ein Teil der Einjährigen nicht bei uns eintrifft. Vielleicht laichen diese anderswo, vielleicht auch nehmen sie gar nicht am Laichzuge teil. Wenn letzteres zutrifft, ist es sehr gut möglich, dass unter ihnen ein weit grösserer Bruchteil Unreifer vorkommt als unter den von uns untersuchten einjährigen Tieren.

Im Juli und August tritt eine Rückbildung des Hodens ein, die sich allerdings nur durch geringere Grösse des Organs, vor Allem durch eine kleinere Breite, kennbar macht (vgl. Abb. 9). Wie weit diese Rückbildung geht, müssen wir dahingestellt sein lassen, da Winterbeobachtungen der 1¼ bis 1½ Jahre alten Tiere völlig fehlen. Die Beobachtungen an Jungtieren lassen vermuten, dass der Hoden im zweiten Winter eine ziemlich hohe Entwicklungsstufe behält. Trotzdem ist es klar, dass die Hodenentwicklung einer deutlichen Periodizität unterliegt und ihren Gipfelpunkt in den Monaten April bis Juni erreicht.

Die zweijährigen Kalmare machen im Sommerhalbjahr eine ähnliche Entwicklung durch wie die hier behandelten einjährigen. Auch ihr Hoden ist bei der Ankunft gross und verkleinert sich im Spätsommer (Abb. 9). Unentwickelte Stücke kommen unter ihnen nicht vor.

Wie der Hoden, so sind auch die übrigen Geschlechtsorgane bei den Sommertieren stark entwickelt. Das Vas deferens ist ganz geschwollen und sieht milchig aus. Im Spermatophorenorgan werden meistens einige halbausgebildete Spermatophoren gefunden. Der Spermatophorensack ist meistens stark ausgewachsen und enthält eine erheblich grössere Menge von Spermatophoren als bei den Wintertieren. Diese haben sich also zwischen Dezember und April gebildet. Nur bei den vereinzelten unreifen Stücken findet diese Bildung nicht statt; bei diesen Tieren sind denn auch all die hier genannten Organe unentwickelt und leer.

Während der Sommermonate wurde der Füllungsgrad der Spermatophorensäcke von rd. 4500 Tieren notiert. Die Bestimmung geschah schätzungsweise; dabei wurden folgende Stufen unterschieden: „voll", „halbvoll", „viertelvoll", „fast leer" und „leer". Diese Benennungen beziehen sich nicht auf die absolute, sondern auf die relative Menge des Inhalts, d.h. sie berücksichtigen die Grösse des Tieres. Einige dieser Stadien sind auf Abb. 9 eingezeichnet.

Es ergab sich in erster Linie, dass die Spermatophorensäcke der einjährigen Tiere bei ihrer Ankunft durchschnittlich, auch relativ gesprochen, weniger voll sind als die der zweijährigen. Dies zeigt sich am besten bei Betrachtung folgender Werte, die sich auf zwischen dem 23. IV. und 20. V. 1935 gesammelte Tiere beziehen:

Von den 49 vollen Tieren mass	24%	10–17 cm	76%	18–30 cm
89 halbvollen	25%		75%	
186 viertelvollen	39%		61%	
41 fast leeren	66%		34%	
4 leeren	(100%)		(0%)	

Die Bereiche 10–17 cm und 18–30 cm sind so gewählt, dass in ersteren die Mehrzahl der Einjährigen, in letzteren die der Zweijährigen fällt.

Wir können dies auch folgendermassen formulieren:

Von 138 Tieren von 10–17 cm war:	Von 231 Tieren von 18–30 cm war:	
9%	16%	voll
16%	29%	halbvoll
53%	49%	viertelvoll
19%	6%	fast leer
3%	0%	leer

Dass der beschriebene Zusammenhang zwischen der Grösse der Tiere und dem Füllungsgrad der Spermatophorensäcke statistisch gesichert ist, geht hervor aus der folgenden Berechnung, die sich auf die Periode 23. IV.–2. V. 1935 bezieht. Es wurden damals eingeliefert: 39 volle Tiere mit einer Durchschnittslänge von 19.5 cm (Standartdeviation $\sigma_{\bar{x}} = 0.64$) und 37 fast leere Tiere mit 16.0 cm Durchschnittslänge ($\sigma_{\bar{y}} = 0.71$). Die Standartdeviation der Differenz ist nach $\sigma_d = \pm\sqrt{\sigma_{\bar{x}}^2 + \sigma_{\bar{y}}^2} = 1.0$ cm und weniger als ein Drittel der Differenz, welche deshalb statistisch gesichert ist.

Die zweijährigen Tiere haben also im Vorsommer relativ mehr gefüllte Spermatophorensäcke als die einjährigen. In anderer Hinsicht verhalten sich die beiden Jahresklassen ähnlich und deshalb werden wir sie im Folgenden zusammen behandeln, zumal man nicht von jedem Stücke das Alter bestimmen kann.

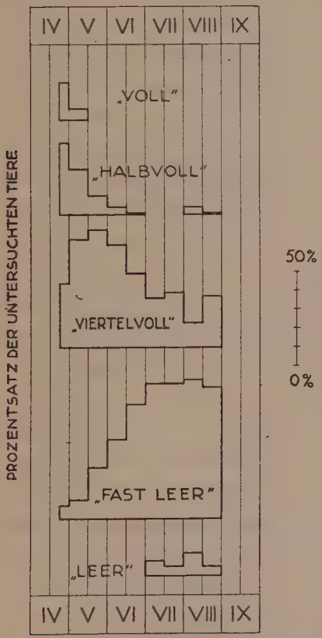

Abb. 10. Füllungsgrad des Spermatophorensackes im Laufe der Zeit, 1934–1940.

Wir sahen schon, dass bei Ankunft der Tiere die Spermatophorensäcke mehr oder weniger gefüllt sind. Bald nachher nimmt nun die Zahl der Tiere mit weniger gefülltem Sack zu. Abb. 10 zeigt, dass diese Zunahme vom April bis wenigstens zur zweiten Junihälfte fortschreitet. Im August kommen einige Abweichungen vor, was vielleicht mit der geringen Zahl der untersuchten Tiere zusammenhängt.

Zwei Faktoren sind verantwortlich für diese Veränderungen. In erster Linie die relative Zunahme der Zahl der einjährigen Tiere im Laufe des Jahres (S. 225). Wir sahen eben, dass diese weniger voll sind als die zweijährigen. Daher muss die Änderung der Populationszusammensetzung einen kleineren mittleren Füllungsgrad hervorrufen.

Diese Änderung ist jedoch zu klein um die ganze Abnahme zu erklären. Als zweite, wichtigere Ursache sind denn auch die den ganzen Sommer hindurch vorkommenden Begattungen zu nennen, die bei der Behandlung der ♀♀ weiter besprochen werden.

Der Verlauf des Füllungsgrades des Spermatophorensackes zeigt also, dass vor der Ankunft der Tiere die Produktion an Spermatophoren den Verbrauch und nachher der Verbrauch die Produktion übertrifft. Demnach könnte es sein, dass überhaupt während des Sommers keine Spermatophoren gebildet werden und dass die Tiere eine am Anfang der Fortpflanzungsperiode aufgespeicherte Reserve aufzehren. Letzteres ist jedoch bestimmt nicht der Fall: den ganzen Sommer hindurch kann man die sich entwickelnden Spermatophoren in den verschiedenen Abschnitten des Spermatophorenorgans finden, wie wir schon S. 234 feststellten.

Bei *Loligo pealii* geschieht Ähnliches, wie man aus Drews (1919) schöner Arbeit über Bau und Bildung der Spermatophoren dieser Art ersehen kann.

Wie schon erwähnt, bezieht sich Obengesagtes auf ein- und zweijährige Tiere zusammen. Von beiden Jahresklassen kommen also die Individuen mehr oder weniger gefüllt an und ihre Spermatophorensäcke werden im Laufe des Sommers immer leerer. Es ist nun nicht mit Gewissheit zu sagen, ob die ausgelaichten einjährigen Tiere im nächsten Frühling wieder reif werden, oder ob die reifen zweijährigen ♂♂ gerade diejenigen Stücke sind, die in ihrem ersten Jahre eventuell nicht gereift und nicht ins Laichgebiet gewandert sind (vgl. S. 233). In beiden Fällen ist es aber klar, dass die geschlechtliche Tätigkeit an eine bestimmte Jahreszeit gebunden ist; wir kommen hierauf zurück.

Die Beobachtungen über den Gonadenzyklus der Weibchen lassen wir hier anschliessen. Wie bei den ♂♂ empfindet man auch hier die Schwierigkeit, dass die Tiere nur während einiger Monate in genügender Zahl im Beobachtungsgebiet verbleiben.

Einige der zu beschreibenden Stadien sind auf Abb. 11 in halbschematischer Weise dargestellt.

Die wenigen jungen Herbst- und Wintertiere, die zur Beobachtung kamen, waren verhältnismässig schwächer entwickelt als die zur selben Zeit gesammelten ♂♂. Sowohl die am 24. X. 1934 als die im Dezember 1939 empfangenen Tiere hatten ein sehr

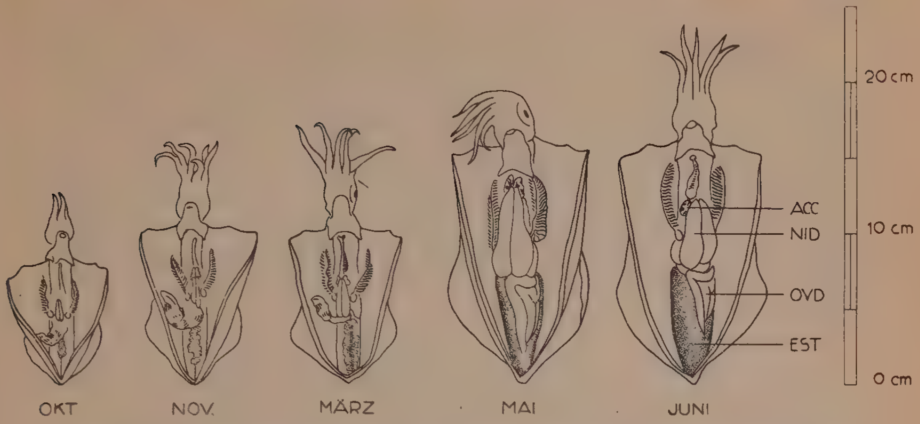

Abb. 11. Gonadenzyklus der ♀♀ vom Oktober des Geburtsjahres bis zum nächtsten Juni. Est = Eierstock, Ovd = Ovidukt, Nid = Nidimentaldrüsen, Acc = Akzessorische Drüsen. Füllungsgrad der Ovidukte: Mai „voll'', Juni „mässig''.

kleines Ovar, dessen körnige Struktur makroskopisch kaum sichtbar war. Bei mikroskopischer Untersuchung waren die noch etwa 0.2 mm grossen Eier gut wahrnehmbar. Die Nidimentaldrüsen waren erst im Anfang ihrer Reifung (allerdings bei den Dezembertieren grösser als bei den Oktobertieren); die akzessorischen Drüsen gleichfalls. Der Ovidukt enthielt begreiflicherweise noch keine reifen Eier und die Spermatheca war makroskopisch nicht sichtbar.

Sogar ein Märztier war noch kaum weiter entwickelt, hatte aber eine sehr geringe Länge und mag deshalb später in seiner Entwicklung als die Mehrzahl seiner Altersgenossen gewesen sein.

Ganz anders sehen dagegen die in der zweiten Aprilhälfte erscheinenden ♀♀ – jetzt ¾ Jahre alt – aus. Die Nidimentaldrüsen sind völlig ausgewachsen und geschwollen; dasselbe gilt für akzessorische und Oviduktdrüse. Auf der Mundmembran ist die Spermatheca als ein kleiner Wulst sichtbar und das Ovar füllt einen Teil des Abdomens mit seinen 1–2 mm grossen Eiern. Links vorn gegen dieses Organ liegt in mehreren Schlingen der Ovidukt mit klaren hellgelben zu Reihen geordneten Eiern, die mithelfen den Abdominalraum prall zu füllen.

Bis zum Verschwinden der Tiere im Spätsommer bleibt der Eierstock stark bis ziemlich stark entwickelt; eine Abnahme gegen Ende der Zeit, wie sie der Hoden aufweist, konnte nicht mit Sicherheit festgestellt werden.

In der zweiten bis dritten Maiwoche erscheinen in kleiner Zahl Weibchen, bei denen die Eier nicht so fest aufeinander gepackt im Ovar liegen wie vorher, wodurch der Eierstock ein auffällig lockeres, unordentliches Aussehen erhält. Wir werden S. 240 hierauf zurückkommen und sehen, dass dies wahrscheinlich die ♀♀ sind, die soeben ihr Gelege abgesetzt haben. Sie kommen den ganzen Sommer hindurch vor.

Auch bei den ♀♀ kommen einjährige Tiere mit unentwickelter Gonade vor. Ihr Ovar ist dem der Wintertiere (siehe oben) sehr ähnlich. Dasselbe gilt für die nidimentalen und akzessorischen Drüsen.

In den Jahren 1935–'40 betrug die Zahl solcher unreifen ♀♀ 16 von 3505 untersuchten Exemplaren. Sie waren, im Gegensatz zu den unreifen ♂♂, die nach dem Obengesagten erst in den Monaten Juli und August auftraten, im Monat Mai am häufigsten. Ihre Länge betrug 9.8–14.7, durchschnittlich 11.5 cm; sie war also, wie bei den unreifen ♂♂, erheblich geringer als die der übrigen Einjährigen, welche nach S. 223 in dieser Zeit auf 13–14 cm geschätzt werden kann.

Herbst- und Winterbeobachtungen über die weitere Entwicklung des Ovars fehlen leider. Im nächsten Sommer haben die zweijährigen ♀♀, wie die einjährigen, zur Zeit ihres Eintreffens einen stark entwickelten Eierstock. Auch bei ihnen ist eine Rückbildung zu Ende des Sommers nicht festzustellen. Unentwickelte Stücke scheinen nicht vorzukommen, genau wie wir dies für die ♂♂ fanden.

Der als Speicherorgan der reifen Eier fungierende Ovidukt zeigt im Laufe des Sommers einen stark schwankenden Füllungsgrad. Letzterer wurde, wie beim Spermatophorensack der ♂♂, für jedes untersuchte Stück aufgezeichnet, wobei die folgenden Abstufungen unterschieden wurden: „viele" (= „voll"), „mässig", „wenig" und „keine" Eier (= „leer"). Auch hier wurde beim Schätzen der Eiermenge der Grösse des Tieres Rechnung getragen.

Wie bei dem Spermatophorensack der ♂♂ steht der Füllungsgrad in Zusammenhang mit der Länge des Tieres.

Zwischen dem 20. IV. und 11. V. 1937 wurden z.B. untersucht:

16 ♀♀	„voll"	durchschn. Länge	16.2 cm	$\sigma_{\bar{x}} = 0.4$ cm
78 ♀♀	„mässig"		14.8 cm	
28 ♀♀	„wenig"		14.7 cm	$\sigma_{\bar{y}} = 0.27$ cm
9 ♀♀	„leer"		12.4 cm	$\sigma_{\bar{z}} = 0.4$ cm

Die Unterschiede in Durchschnittslänge zwischen den ♀♀ der ersten und dritten, der ersten und vierten und der dritten und vierten Gruppe sind statistisch gesichert, da sie grösser sind als 3 × σ_d (berechnet nach

$\sigma_d = \pm \sqrt{\sigma_x^2 + \sigma_y^2}$). Dagegen besteht kein wesentlicher Unterschied zwischen den ♀♀ mit mässig viel Eiern und denen mit wenig Eiern.

Auf S. 223 sahen wir, dass die zweijährigen ♀♀ zwischen dem 20. IV. und dem 20. V. durchschnittlich etwa 17 cm lang sind. Unter den vollen Tieren der obigen Tabelle findet sich also ein höherer Prozentsatz zweijähriger als unter den weniger gefüllten, m.a.W.: die zweijährigen ♀♀ tragen, auch wenn man mit ihrer Grösse rechnet, mehr Eier im Ovidukt als die einjährigen, wie auch die zweijährigen ♂♂ verhältnismässig mehr gefüllte Spermatophorensäcke als die einjährigen haben (S. 235).

Auch bei vielen Fischarten nimmt die Eierzahl mit steigendem Alter der Tiere zu (so z.B. bei *Acanthias vulgaris* Risso, vgl. Ford 1921). Ähnliches hat man bei einigen Vogelarten, die in mehreren Jahren ihres Lebens zur Fortpflanzung schreiten, festgestellt. So wissen wir vom Star (*Sturnus vulgaris*) (Kluyver 1935), Singammer (*Melospiza melodia*) (Nice 1937) und vom Gartenrotschwanz (*Phoenicurus phoenicurus*) (Ruiter 1941), dass die mehrjährigen ♀♀ mehr Eier legen als die einjährigen. Ob aber bei diesen drei Vogelarten – und auch bei *Loligo vulgaris* – die Eierproduktion bei zunehmendem Alter stetig zunimmt, ist nicht bekannt und lässt sich auch nicht leicht bestimmen, da sie im Freien durchschnittlich nur ein relativ kurzes Alter haben. Man würde erwarten, dass die Eierproduktion anfangs stieg um im höheren Alter wieder abzunehmen.

Wie bei den ♂♂ werden wir im Folgenden ein- und zweijährige ♀♀ zusammen betrachten. Eine Trennung ist auch wohl kaum möglich, da die Masse der beiden Jahresklassen zu wenig verschieden sind und andere Merkmale zur Beurteilung des Alters nicht vorliegen.

Die Änderungen des Füllungsgrades der ♀♀ im Laufe der Zeit sind in Abb. 12 graphisch dargestellt. Der Prozentsatz der Tiere mit vollem bis mässig gefülltem Ovidukt ist anfangs hoch, ziemlich bald nach dem Eintreffen der Tiere werden aber die Individuen mit wenig gefülltem Ovidukt häufiger. Vermutlich wird dies, wie bei den ♂♂, nur zu einem geringen Teil von der Änderung in der Populationszusammensetzung bedingt, während die Eiablage die Hauptursache sein wird. Zu dieser Zeit bringen auch die Fischer die ersten Eiertrauben an (1933: 9. V., 1934: 12. V., 1935: 18. V., 1936: 5. V., 1937: 4. V.).

Die relative Zunahme der Zahl der weniger gefüllten Tiere hört in der zweiten Maihälfte auf. Wir können also folgern, dass vor dem Erscheinungsdatum der Tiere die Eierproduktion den Verbrauch, dann bis Ende Mai der Verbrauch die Produktion

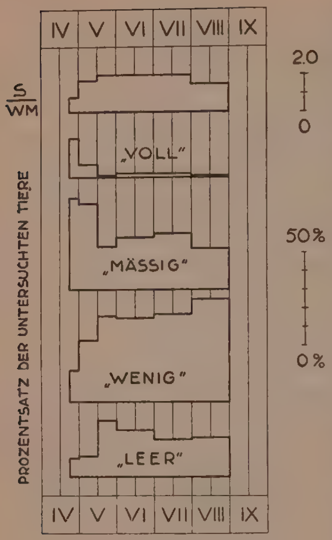

Abb. 12. Verhältniszahl $\frac{S}{WM}$ und Füllungsgrad des Oviduktes im Laufe der Zeit, 1934–1940.

übertrifft und dass schliesslich die beiden sich ausgleichen. Und zwar ist der Verbrauch vor dem Erscheinen der Tiere gleich Null zu setzen, da die Eier nur im Küstenmeer abgelegt werden (wo die ersten Anfang Mai gefunden werden). Vom Mai bis etwa Anfang August werden stetig Eier verbraucht, wie uns die Funddaten frisch abgelegter Eier zeigen (Tabelle 2).

Die Eiablage dauert also von Mai bis Juli oder August, d.h. fast ebensolange wie die Tiere im Küstengebiet bleiben und während dieser ganzen Zeit liefert das Ovar dem Ovidukte seine Eier ab. (Die Zahl der laichenden ♀♀ erreicht übrigens ihren Gipfelpunkt in der 2. Maihälfte, S. 245).

Wir fanden schon, dass Mitte Mai Weibchen erscheinen, deren Ovar locker und eigenartig uneben aussieht, während ihr Ovidukt wenige oder fast keine Eier enthält. Wir zweifeln nicht daran, dass dies Weibchen sind, die ihre Eier kurz vorher absetzten. Ein ziemlich grosser Prozentsatz derselben hat ausserdem neuabgesetzte Spermatophoren auf dem Spermathecahügel, zum Zeichen, dass der Eiablage oft eine Kopulation folgte.

TABELLE 2

Entwicklungszustand der Eier

Monat (1933–'37)	Zahl der gesammelten Eiertrauben	Hiervon untersucht:		
		Unentwickelt, frisch	Entwickelt	Leer und verfault
IV.	0	—	—	—
V.	30	13	1	6
VI.	37	—	—	—
VII.	37	15	16	6
VIII.	46	4	1	21
IX.	0	—	—	—

Solche ♀♀ mit lockerem Ovar und sehr wenig gefülltem Ovidukt, die also vorkommen ab Mitte Mai und den ganzen Sommer hindurch anwesend bleiben, sind nie zahlreich, sie bilden immer nur einen kleinen Prozentsatz aller Tiere; am häufigsten sind sie wohl in der zweiten Maihälfte, zweifellos weil dann so viele ♀♀ zu gleicher Zeit ihre Eier ablegen. Ab Mitte Mai kommen neben diesen ♀♀ mit lockerem Ovar ziemlich viele vor, die wie diese nur wenige Eier im Ovidukt haben, deren Ovar aber normal aussieht. Wir nehmen an, dass dies Tiere sind, deren Ovar sich sozusagen regeneriert hat und bei denen sich das Ovidukt wieder füllt. Allem Anschein nach findet die Entleerung des Oviduktes von nun an schon statt, wenn die Zahl ihrer Eier bis „mässig" gestiegen ist, denn ♀♀ mit „vollem" Ovidukt kommen nach Mitte Mai nur noch in sehr kleiner Anzahl vor. Die Tiere würden also mehrere Gelege produzieren, von denen das erste das grösste ist. Die Zahl der Gelege lässt sich nicht bestimmen.

Die Entwicklung des Ovidukts im Herbst und Winter ist uns unbekannt. Eier werden in dieser Zeit bestimmt nicht abgelegt. Ob die Eierproduktion im Winter fortschreitet oder zu welcher Zeit im Frühling die Ovidukte sich zu füllen anfangen, wissen wir nicht. Auch wissen wir nicht, ob jedes ♀ ein- oder zweimal in ihrem Leben zur Fortpflanzung schreitet. Es wäre nämlich möglich, dass die zweijährigen Tiere die unentwickelten einjährigen des Vorjahres sind. Wir selbst halten diese Möglichkeit aber für unwahrscheinlich.

Die Untersuchung der weiblichen Geschlechtsorgane umfasste schliesslich noch Beobachtungen über den Zustand der Spermatheca und über die Anwesenheit frisch abgesetzter Spermatophoren in deren Nähe. Es ist ja aus den Arbeiten LAFONTS (1871), DREWS (1911) und VAN OORDTS (1939) bekannt, dass bei *Loligo pealii* Les. und *Loligo vulgaris* Lam. die Spermatophoren während der Begattung auf die Mundmembran abgesetzt werden [1]). Sie entleeren sich hier bald; die Spermatozoen gelangen dann in die Spermatheca (= Receptaculum seminis), eine drüsige Höhle in jener Membran. Diese Spermatheca sieht in gefülltem Zustande milchig weiss aus; wir sprechen dann von einem „weissen Mundhügel”. Die leeren oder halbleeren Reste der Spermatophoren kleben zuerst im Hautschleim der Mundmembran, verschwinden dann aber, noch bevor der Inhalt der Spermatheca verbraucht ist.

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[1]) Für *Loligo pealii* stellte DREW (1911) ausserdem Begattungen fest, bei denen die ♂♂ die Spermatophoren in der Mantelhöhle des ♀ absetzen. Bei den ♀♀ von *L. vulgaris* aus der Umgebung von Den Helder fanden wir, obgleich einige Tausende Stücke untersucht wurden, niemals Spermatophoren in der Mantelhöhle. LEBERT und ROBIN (1845) geben aber eine deutliche Beschreibung und Abbildung eines ♀ dieser Art, das explodierte Spermatophoren an der Innenwand des Mantels trug. Die Herkunft dieses Tieres ist unbekannt.

Aus unseren Beobachtungen ging in erster Linie hervor, dass die übergrosse Mehrzahl der reifen ♀♀ eine gefüllte Spermatheca hat. An zweiter Stelle zeigten sie, wie sich die Frequenz der Begattungen im Laufe der Zeit entwickelte. Wenn nämlich wenige Begattungen vorkommen, verlieren viele ♀♀ die Spermatophorenreste. Es gibt dann verhältnismässig viele ♀♀ mit gefüllten Spermatheken, doch ohne Spermatophorenreste. Andrerseits kommen in Perioden von vielen Begattungen relativ viele ♀♀ vor, die Spermatophorenreste tragen. Bestimmt man nun das Verhältnis zwischen der Zahl der ♀♀ mit Spermatophorenresten und der Zahl der ♀♀ ohne solche, doch mit sogenanntem weissem Mundhügel, d.h. mit gefüllter Spermatheca oder, kurz gesagt, $\frac{S}{WM}$[1]), so hat man ein mehr oder weniger genaues Mass für die Frequenz der Begattungen. In Abb. 12, oben, ist der Verlauf dieser Verhältniszahl dargestellt. Sie steigt zuerst schnell, später langsamer und nimmt in August ein wenig ab. Wir können hieraus folgern, dass sich die Tiere von der Ankunft an und fast bis zu ihrem Abzug mit unverminderter Kraft begatten. Diese Folgerung bezieht sich auf die Zahl der Begattungen pro anwesendem reifem Weibchen; die Zahl der überhaupt vorkommenden Begattungen hat ein ausgeprägtes Maximum in der zweiten Maihälfte, wenn die Zahl der anwesenden Tiere ihren Höhepunkt erreicht.

Wir wollen diese Beobachtungen über die Periodizität der Fortpflanzung noch einmal zusammenfassen. Im Dezember ist das Ovar noch sehr wenig entwickelt und im Ovidukt finden sich dann noch gar keine Eier. Die Eiablage geschieht nur vom April bis zum August mit einem Maximum in der zweiten Maihälfte. Genau dieselbe Periodizität zeigen die Begattungen und deshalb der Spermatophorenverbrauch. Der Hoden dagegen produziert bereits im Oktober Spermatozoen, die schon ab Dezember in Spermatophoren aufgespeichert werden.

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[1]) Wir verwendeten die Verhältniszahl $\frac{S}{WM}$ und nicht $\frac{S}{\text{Summe der untersuchten ♀♀}}$ da sonst die Anwesenheit unreifer ♀♀ die Werte beeinflusst hätte.

Was Letzteres anbelangt, benehmen andere periodisch reifende Tierarten sich ganz verschieden. Im Vogelhoden z.B. entwickeln sich die Spermatozoen erst kurz vor der Paarungszeit um bald danach wieder zu verschwinden. Man könnte annehmen, dass die frühe Reifung des ♂ Kalmars – lange Zeit vor der Begattungsperiode – in Zusammenhang steht mit der Fähigkeit, das Sperma in Spermatophoren aufzuspeichern. Eine Vergleichung mit anderen Tierarten mit Spermatophoren wäre hier interessant.

Es ist schliesslich interessant, die Fortpflanzungszeit von Kalmaren anderer Fundorte, sowie anderer Cephalopodenarten zum Vergleich heranzuziehen. Leider liegen nur wenige Daten vor.

Lo Bianco (1909) beschreibt, dass im Mittelmeer die Eier von *Loligo vulgaris* zwischen November und Juli und am meisten von März bis Juni gefischt werden. (Hinzugefügt sei, dass die Art im Mittelmeer das ganze Jahr hindurch anwesend ist). Die Fortpflanzung dauert hier also länger und findet früher im Jahre statt. Einige andere Cephalopodenarten zeigen im Mittelmeergebiet gleichfalls eine periodische Fortpflanzung. Lo Bianco erwähnt: *Sepia officinalis* L. XII.–VII., selten VIII., X., XI., Eier vor Allem III.–VI. häufig; *Octopus vulgaris* Lam. Eier V.–VIII.; *Eledone moschata* Lam. IV.–VII. Bei *Sepia* dauert die Fortpflanzungszeit, wie bei *Loligo vulgaris*, im Mittelmeer erheblich länger als in der Nordsee, wo sie nach unseren Beobachtungen nur vom Mai bis zum August dauert. *Loligo marmorae* Ver. laicht im Mittelmeer sogar das ganze Jahr hindurch; die Art ist nach einigen Autoren mit *Alloteuthis subulata* Lam. aus dem Nordseegebiet identisch. Letztere laicht im Winter nicht. Wir hätten hier also vielleicht mit einem Beispiel zu tun, bei welchem die Periodizität im Norden stark auffällt, im Süden offenbar fast oder ganz fehlt. Ähnliches beschreibt Sasaki (1921) vom japanischen *Ommastrephes sloani pacificus*: in Südjapan soll die Paarzeit das ganze Jahr hindurch dauern (allerdings mit einem Maximum im Sept.-Okt.), während sie in Nordjapan auf den Dezember beschränkt sein soll. Jedoch scheint letztere Folgerung uns nicht zwingend, weil in Nordjapan in verschiedenen Monaten nur halbwüchsige Tiere untersucht wurden.

Wie bei allen periodischen Erscheinungen fragt es sich, von welchen äusseren Faktoren der Rhythmus der Fortpflanzung bei *Loligo* bedingt wird. Anscheinend liegen hier andere Verhältnisse vor als bei vielen Vögeln der gemässigten Zonen, deren Reifung durch die steigende tägliche Beleuchtungsdauer herbeigeführt wird (Rowan 1938). Denn der Kalmar fängt seine Fortpflanzung im Süden bei abnehmender, im Norden bei zunehmender Tageslänge an. Am wahrscheinlichsten kommt uns eine Regulierung der Periodizität vor, bei der zur Fortpflanzung ein bestimmter Temperaturbereich erforderlich ist, dessen obere Grenze im Mittelmeergebiet zwischen Juli und November überschritten und dessen untere Grenze im Nordseegebiet erst Ende April erreicht wird. Besonders die längere Dauer der Fortpflanzungsperiode im Süden deutet auf überzeugender Weise auf einen Einfluss der Temperatur hin. Man findet diese längere Fortpflanzungsdauer im Süden auch bei anderen Tieren mit südlicher Verbreitung (die also eine hohe Temperatur zu ihrer Fortpflanzung brauchen), z.B. den Medusen (VERWEY 1943) und Fischen (*Engraulis encrasicholus* (L.), *Clupea pilchardus* Walb.: FAGE, 1920, p. 14 und 42).

Wir sahen oben, dass das Laichgeschäft von *Loligo vulgaris* anfängt, sobald die Tiere ins Küstengebiet eingewandert sind, und fast bis zum Abzug der letzten Stücke fortgesetzt wird. Wir wissen ausserdem, dass die Fortpflanzung nicht oder nicht nennenswert ausserhalb des Küstengebiets stattfindet. Zuzug und Abzug fallen also, wenigstens ungefähr, mit Anfang und Ende der Fortpflanzung zusammen. Ferner wissen wir, dass im Laichgebiet nur sehr wenige unreife Stücke vorkommen. Dies alles sieht aus, alsob ein direkter Zusammenhang zwischen Reifheit und Zug besteht, wie dieser schon seit Jahren für Vögel angenommen wurde. Hier hat man in einem Falle sogar experimentell bewiesen, dass sowohl die Reife wie der Frühlingszug von der Zunahme der Tageslänge ausgelöst werden (ROWAN 1938). Dabei nahm man anfangs an, dass die Lichtzunahme die Geschlechtsreife verursache und diese wiederum das Erwachen des Zugtriebes. Nicht zu verstehen ist dann aber, wie die einjährigen, nicht geschlechtsreifen Jungen mancher Arten (*Sepia*, bestimmte Fische, viele Watvögel, u.a.) am Zuge teilnehmen können. Seit PUTZIG (1939) zeigte, dass kastrierte Krähen den Frühlingszug ausführen, ist die Erscheinung denn auch wahrscheinlich so zu deuten, dass Geschlechtsreife und Zugtrieb von einer gemeinsamen Ursache, der zunehmenden Tageslänge, ausgelöst werden. In ähnlicher Richtung, dass nämlich Reife und Zugtrieb von ein und derselben Ursache ausgelöst werden, müssen vielleicht auch die genannten Zusammenhänge im Falle von *Loligo* gesucht werden.

Beim Zuge erreichen die Tiere also ihre Laichgebiete. Der Funktion nach kann man also von Laichzug sprechen. Hiermit wollen wir aber nicht behaupten, dass der Zug nur diese Bedeutung hat. Letzteres würde sogar sehr unwahrscheinlich sein, da meistens mehrere Funktionen zusammengehen. So ist z.B. der Effekt der bekannten nach Norden gerichteten Frühlingswanderungen vieler Tierarten (Vögel) einerseits, dass die Fortpflanzungsgebiete erreicht werden, andrerseits, dass die dort im Sommer aufblühenden Nahrungsvorräte für die Art aufgeschlossen werden, während es wahrscheinlich ist, dass auch günstigere Temperaturverhältnisse gefunden werden. Wir werden S. 276 sehen, dass auch bei *Loligo vulgaris* wahrscheinlich der Zug mehreren Funktionen dient. Der Umstand, dass im Allgemeinen mehrere Funktionen zusammengehen, macht es unmöglich, die oft verwendete Einteilung der Tierwanderungen nach der Funktion aufrechtzuhalten.

4. DIE PERIODIZITÄT DES ZUGES

Aus dem Verlauf der Fangzahlen (Abb. 13) können wir folgern, dass bei Den Helder im Allgemeinen die Einwanderung von der zweiten Aprilhälfte bis Ende Mai die Auswanderung übertrifft und dass von Ende Mai bis Ende August umgekehrte Verhältnisse herrschen, ohne dass in der Zwischenzeit ein stationnärer Zustand, wie wir diesen bei vielen Zugvögeln sehen, eingetreten ist. Wir halten es sogar für wahrscheinlich, dass seit frühester Zeit auch Auswanderung stattfindet und dass gleichfalls auch nach der zweiten Maihälfte fortwährend neue Stücke einwandern. Begreiflicherweise erlauben die Fangzahlen aber nur Schlüsse über die Differenz von Ein- und Auswanderung und nicht über deren absolute Grösse.

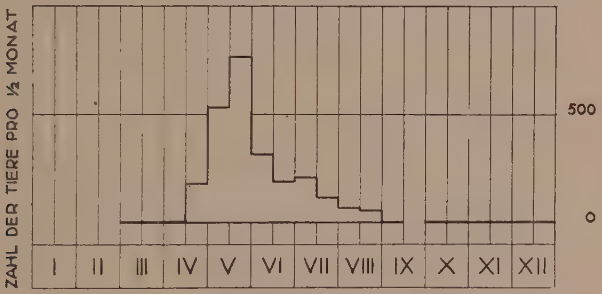

Abb. 13. Fangzahlen von Kalmaren. Durchschnittswerte 1933–1940.

Die Fangzahlen der einzelnen Jahre geben im Allgemeinen das gleiche Bild und sind hier nicht dargestellt worden. Es fällt auf, dass das Anfangsdatum des Zuges in den verschiedenen Jahren nur innerhalb enger Grenzen schwankt. Allerdings zeigen die Erscheinungsdaten der Einzeltiere eine grosse Streuung, wie aus Tabelle 3 hervorgeht, doch dies kann kaum verwundern, da neben ihrer Anwesenheit der Zufall in starkem Masse ihre erste Erbeutung bestimmt. Fügen wir dagegen die Daten zusammen, an denen eine etwas stärkere Einwanderung festgestellt wurde, z.B. die Tage, an denen zum ersten Male je 5 oder je 10 Tiere eingeliefert wurden, so finden wir nur eine geringe Streuung: im ersteren Falle 13.–30. IV., im letzteren 20.–30. IV. Wir können also feststellen, dass der Anfang eines stärkeren Zuzuges auf die zweite Aprilhälfte beschränkt ist und von Jahr zu Jahr nur wenig schwankt. Letzteres gilt bekanntlich für die Wanderungszeiten mehrerer Tierarten. Der Frühlings- und Herbstzug mancher Vogelarten liefern davon viele Beispiele.

TABELLE 3

Erscheinungsdaten von *Loligo vulgaris*

Jahr	Wenigstens 1 Stück	Wenigstens 5 St.	Wenigstens 10 St.
1933	13. IV., 20. IV.	20. IV.	20. IV.
1934	21. IV., 23. IV.	25. IV.	25. IV.
1935	20. IV., 23. IV.	23. IV.	23. IV.
1936	3. IV., 13. IV.	28. IV.	28. IV.
1937	2. III., 14. IV.	20. IV.	20. IV.
1938	18. III., 12. IV.	13. IV.	22. IV.
1939	15. II., 6. IV.	22. IV.	29. IV.
1940	27. IV., 30. IV.	30. IV.	30. IV.

Der Einfall des stärkeren Zuges scheint meistens ziemlich plötzlich zu verlaufen, denn in 6 der 8 Untersuchungsjahre fallen die Daten, an denen zum ersten Male je 5 bzw. je 10 Tiere erbeutet wurden, zusammen. Nur in den Jahren 1938 und 1939 liegt etwa eine Woche zwischen den beiden Daten. In beiden Jahren trat sofort nach dem Erbeuten der ersten 5 Tiere eine Periode windigen Wetters ein, die einige Tage dauerte. Zweifelsohne ist während dieser Tage die Küstenfischerei, die uns ja die Kalmare liefert, eingestellt worden. Dadurch ist das Datum der ersten 10 Stücke in diesen Jahren unnatürlich verspätet. Wenn auch eine ähnliche Wirkung in den anderen Jahren die Lage des Datums der ersten 5 Stücke beeinflusst haben kann, betrachten wir doch für unsre weiteren Ausführungen das Datum, an dem zum ersten Male je 5 Tiere gefangen wurden, als das zuverlässigste Mass für den Anfang des stärkeren Zuges.

Es ist der Mühe Wert, nach Zusammenhängen zwischen dem

Anfangsdatum des Zuges und den äusseren Faktoren zu suchen. Wir haben zu diesem Zweck in Tabelle 4 die Temperatur und den Salzgehalt beim Haaks-Feuerschiff mit dem Zugbeginn verglichen.

TABELLE 4

Erscheinungsdatum und Umweltfaktoren

	1933	1934	1935	1936	1937	1938	1939	1940
Temp. Haaks 1.–10.III. (°C)	4.8	4.2	6.1	5.6	4.9	5.5	5.8	Kalt. Keine Beobachtungen wegen des Krieges.
11.–20.III.	6.0	4.5	5.5	5.5	5.5	6.1	6.1	
21.–31.III.	6.1	5.2	6.1	6.4	5.8	6.8	6.0	
1.–10.IV.	7.1	5.0	6.4	6.8	6.5	7.3	6.6	
11.–20.IV.	7.6	5.6	7.2	7.1	7.5	7.4	7.8	
21.–30.IV.	8.2	6.4	8.1	7.4	8.0	7.9	8.3	
Erscheinungsdatum (April)	20.	25.	23.	28.	20.	13.	22.	30.
Salin. Haaks 21.–30.IV. (°/₀₀)	34.25	33.30	34.34	34.52	32.94	33.75	33.52	—

Aus dieser Tabelle geht hervor, dass mit dem Salzgehalt der letzten Aprildekade kein Zusammenhang vorliegt. Mit der Temperatur dagegen besteht eine, wenn auch nicht sehr schöne Korrelation, indem die drei Jahre, deren letztes Aprildrittel kalt war (1934, 1936 und 1940), die spätesten Einwanderungsdaten zeigen. Jedoch ist die Temperatur nicht das einzige regulierende Prinzip. Wenn dies der Fall wäre, müssten die Tiere, die im Jahre 1934 bei 6.4° einwanderten, 1933 schon Ende März, 1935 schon Anfang April, 1936 Ende März, 1937 Anfang April, 1938 Mitte März und 1939 Anfang April erschienen sein, was den Tatsachen nicht entspricht. Die Tiere sind also durch andere Faktoren an die zweite Aprilhälfte gebunden und der Einfluss der Temperatur ist nur ein untergeordneter. Nach dem, was von Zugvögeln bekannt ist, liegt es auf der Hand, für diese Bindung an die zweite Aprilhälfte die Tageslänge verantwortlich zu machen, deren grosser Einfluss von ROWAN u. A. festgestellt worden ist.

Unserem Ergebnis entsprechen die Befunde von Frau NICE (1937), die die Phänologie der Singammer (*Melospiza melodia* (Wilson)), einer amerikanischen Zugvogelart, eingehend untersuchte. Nachdem sie nachgewiesen hat, dass die Tiere in wärmeren Jahren verhältnismässig früh, in kälteren Jahren spät an-

kommen, stellt sie fest (S. 49): „That time of year is one of the fundamental factors in Song Sparrow migration is shown by the fact that high temperatures in December, January and early February (d.h. längere Zeit vor der Ankunft der Tiere im letzten Februardrittel) . . . never bring a migration. Migration is conditioned by both lengthening days and temperature." Hinzugefügt sei, dass es allen Anschein hat, dass die von NICE für die Singammer entwickelte Regel auch für den Zug mancher anderen Vogelarten gilt.

5. DIE HÄUFIGKEIT DER LAICHZÜGLER IN VERSCHIEDENEN JAHREN

Bei einer wandernden Tierart wie der unsrigen hängt die Häufigkeit, ausser vom Erfolg der Fortpflanzung in den vorangegangenen Jahren, auch vom Prozentsatz der Tiere ab, welcher am Zuge ins Untersuchungsgebiet teilnimmt. In unserem Falle ist es nicht möglich, die beiden Momente zu trennen. Eine weitere Betrachtung scheint daher ziemlich aussichtslos. Jedoch suchten wir nach Zusammenhängen zwischen der Zahl der jährlich anwesenden Tiere und den Schwankungen des „Unterwasserklimas". Wir beschränkten unsre Berechnungen auf die Monate April und Mai, da die Juniankäufe aus technischen Gründen keine zuverlässigen Daten lieferten. In Tabelle 5 wird die Zahl der Kalmare mit den Salzgehalts- und Temperaturabweichungen des Beobachtungsgebietes verglichen. Letztere wurden in folgender Weise berechnet. Für jeden Monat wurde aus den Beobachtungen vom Marsdiep und aus denjenigen des Haaks-Feuerschiffes (zwei Stationen, die auf der Innen- bzw. Aussengrenze des Verbreitungsgebietes von *Loligo vulgaris* bei Den Helder liegen, siehe Abschnitt 6a) die Differenz gemessener

TABELLE 5

Häufigkeit der Kalmare in verschiedenen Jahren, Temperatur und Salzgehalt

	1933	1934	1935	1936	1937
Durchschn. Salzgehaltsabweichung IV., V. in ‰	+0.7	+0.6	—0.3	0.0	—2.2
Durchschn. Temperaturabweichung IV., V. in °C.	+0.6	—0.1	+0.1	+0.3	+0.5
Zahl der Kalmare IV., V.	2734	877	897	2162	1592

Monatswert minus den monatlichen Durchschnittswert vieler Beobachtungsjahre bestimmt und dann der Mittelwert dieser beiden Abweichungsziffern berechnet. Schliesslich wurde der Durchschnittswert der für April und Mai gefundenen Mittelwerte berechnet.

Es zeigt sich in der Tabelle, dass von den 5 Beobachtungsjahren die wärmeren die grösseren Anzahlen hatten, während ein Zusammenhang mit dem Salzgehalt nicht festzustellen ist. Da man von einer südlichen Art erwarten kann, dass sie eine verhältnismässig hohe Temperatur beansprucht, gewinnt die Erklärung an Wahrscheinlichkeit, dass in warmen Jahren ein grösserer Bruchteil der Kalmare bis auf unsere Breite durchdringt als in kalten. Hierdurch werden dann die grossen Fänge verursacht.

6. DIE VERBREITUNG VON LOLIGO VULGARIS BEI DEN HELDER

a. Die Gebietswahl in ihrer Abhängigkeit von äusseren Faktoren

Bei jedem eingelieferten Stücke meldeten die Fischer den Fundort und die Nummer des Schiffes. Da der Einkaufspreis für Tiere aller Fundorte derselbe war, gab es bei diesen Meldungen keine wesentliche Veranlassung zu Betrug. Trotzdem wurden die Angaben dann und wann durch Nachfrage kontrolliert; es zeigte sich hierbei, dass die Fundorte im Allgemeinen richtig angegeben wurden.

Das von helderschen Schiffen befischte Gebiet gliedert sich in mehrere Teile. Zuerst gibt es die Fischgründe der Küstenfischer; diese sind auf Abb. 14 mit No. 1 bis 7 angegeben. Sie stehen alle mehr oder weniger unter Süsswasser- bzw. Landeinfluss. Man fischt hier mit Schleppnetzen; im Gebiet No. 7 (dem Wattenmeer) ausserdem mit „Kommen" (stehenden Heringnetzen). Mit diesen Küstengebieten fällt das Revier der Hochseefischer z.T. zusammen. Letzteres umfasst neben der Umgebung des Haaks-Feuerschiffes und des Diepe Gat (No. 1 auf Abb. 14) eine grössere Strecke der südlichen Nordsee, deren äussere Punkte etwa Borkum Riff, Klaverbank, Markhams Hole und der Breeveertien querab Egmond sind. In all diesen Gebieten ist die Intensität der Fischerei geringer als in Küstennähe. Man fischt hier zum grössten Teil mit Schleppnetzen.

Für unsre weiteren Betrachtungen spielt fast nur die Küsten-

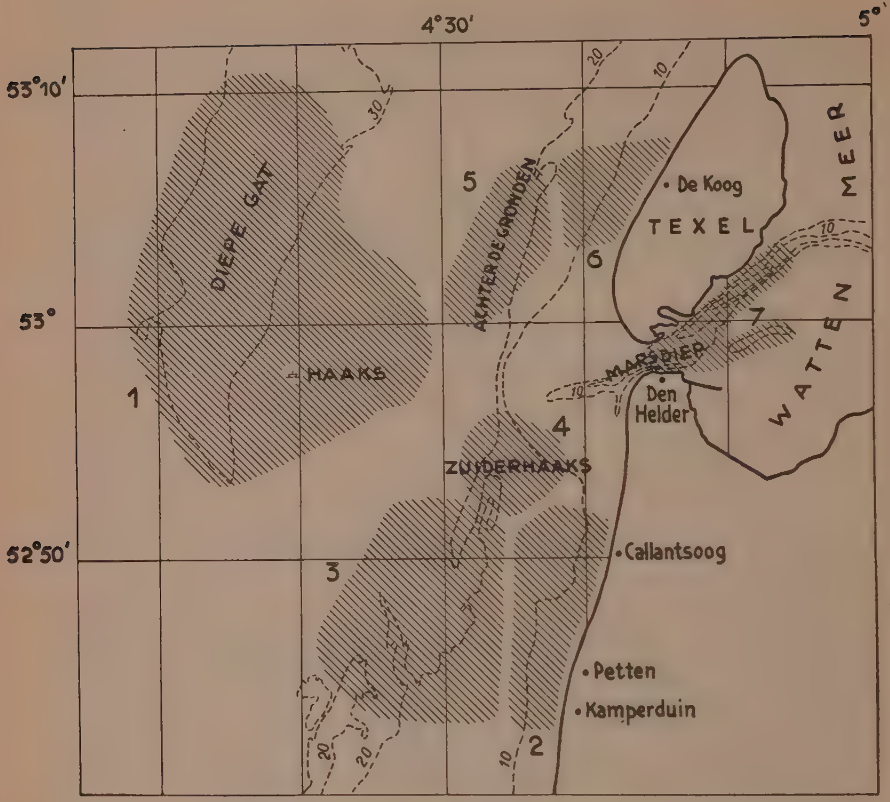

Abb. 14. Das Küstenmeer bei Den Helder mit Angabe der verschiedenen im Text genannten Gebietsteile. Tiefen in m.

zone eine Rolle, denn an diese ist *Loligo vulgaris* im Sommerhalbjahr stark gebunden. Aus dieser erhielt die Zoologische Station 1933–'40 mehr als 12000 Kalmare gegenüber nur 180 (ungefähr 1½%) aus hoher See, d.h. von weiter seewärts als Gebiet No. 1. Ein solches Missverhältnis lässt sich aus der obengenannten geringeren Stärke der Hochseefischerei nicht erklären und kann nur darauf beruhen, dass die Tiere die Küstenzone bevorzugen.

Zur Vergleichung können wir die Fangzahlen einer anderen Art, nämlich die von *Acanthias vulgaris* Risso heranziehen. Auch diese wird regelmässig von der Zoologischen Station eingekauft. In der Periode I. VI.–31. XII. 1938 wurden 110 Stücke von der Küstenzone (Gebiet no. 1–7) und 1313 Stücke von weiter entfernten Stellen eingeliefert, also ein dem von *Loligo vulgaris* fast entgegengesetztes Verhältnis.

Weiter interessiert es, dass sogar die ausserhalb der Küstenzone gefangenen *Loligo vulgaris* immerhin in geringer Entfernung vom Lande erbeutet wurden. Nur einige Winterfänge bilden eine Ausnahme: 24. XI. 1939 2 St. Tea Kettle Hole 20 Fdn., 3 St. 20 Meile NNW vom Feuerschiff Haaks, 15–16 Fdn., 18. XII. 1939 8 St. Tea Kettle Hole 20 Fdn. Hierauf kommen wir später zurück.

Die Ansicht, dass die Art in der Nordsee selten sei (Tesch 1908, Grimpe 1925), ist wahrscheinlich auf dieses Meiden der Hochsee zurückzuführen. Die Forschungsschiffe fischen selten in Küstennähe und daher bekommen die Spezialisten, welche die Ausbeuten derselben untersuchen, die Tiere nicht in die Hände.

Die Ursache der Bindung ans Küstenmeer wird weiter unten untersucht werden. Zuerst betrachten wir das Vorkommen innerhalb des Küstenmeeres etwas eingehender und beschränken uns vorläufig aufs Sommerhalbjahr.

In erster Linie werden wir uns fragen, wo sich in jedem Monat die Hauptmasse der Kalmare findet. Zu diesem Zwecke ist für jeden Sommermonat die Zahl der erbeuteten Stücke pro Gebietsteil berechnet und in Prozenten des monatlichen Gesamtfanges ausgedrückt. Die Prozentsätze sind in Abb. 15a eingetragen. Diese Zahlen würden aber nur dann einen richtigen Eindruck des Vorkommens der Kalmare geben, wenn die Fischerei das ganze Jahr hindurch an den selben Stellen ausgeübt werden würde. Dies ist jedoch nicht der Fall und wir müssen daher auch die Schwankungen der Intensität der Fischerei in Betracht ziehen. Leider fehlen genaue Statistiken, aber die Journale der Zoologischen Station geben doch Anhaltspunkte zur Beurteilung dieser Frage. Denn ausser Kalmaren wurden verschiedene andere Tierarten von den Fischern angebracht. Auch deren Fundorte sind regelmässig aufgezeichnet worden. Um hieraus die zeitliche und örtliche Verteilung der Fischerei zu ermitteln, sind wir folgendermassen verfahren. Für jeden Fundort wurde die monatliche Zahl der Meldungen berechnet und in Prozenten der monatlichen Gesamtzahl ausgedrückt. Abb. 15b bringt das Ergebnis und stellt also die relative Intensität der Fischerei an den verschiedenen Fangorten für jeden einzelnen Sommermonat dar. Diese weist erhebliche Schwankungen auf.

Um nun die relative Häufigkeit der Kalmare festzustellen, müssen wir für jeden Sommermonat und für jeden Fangort den Quotienten $\frac{\text{Zahl der gefangenen Kalmare}}{\text{Intensität der Fischerei (Meldungszahl)}}$ berechnen und den gefundenen Wert in Prozenten der monatlichen Summe dieser

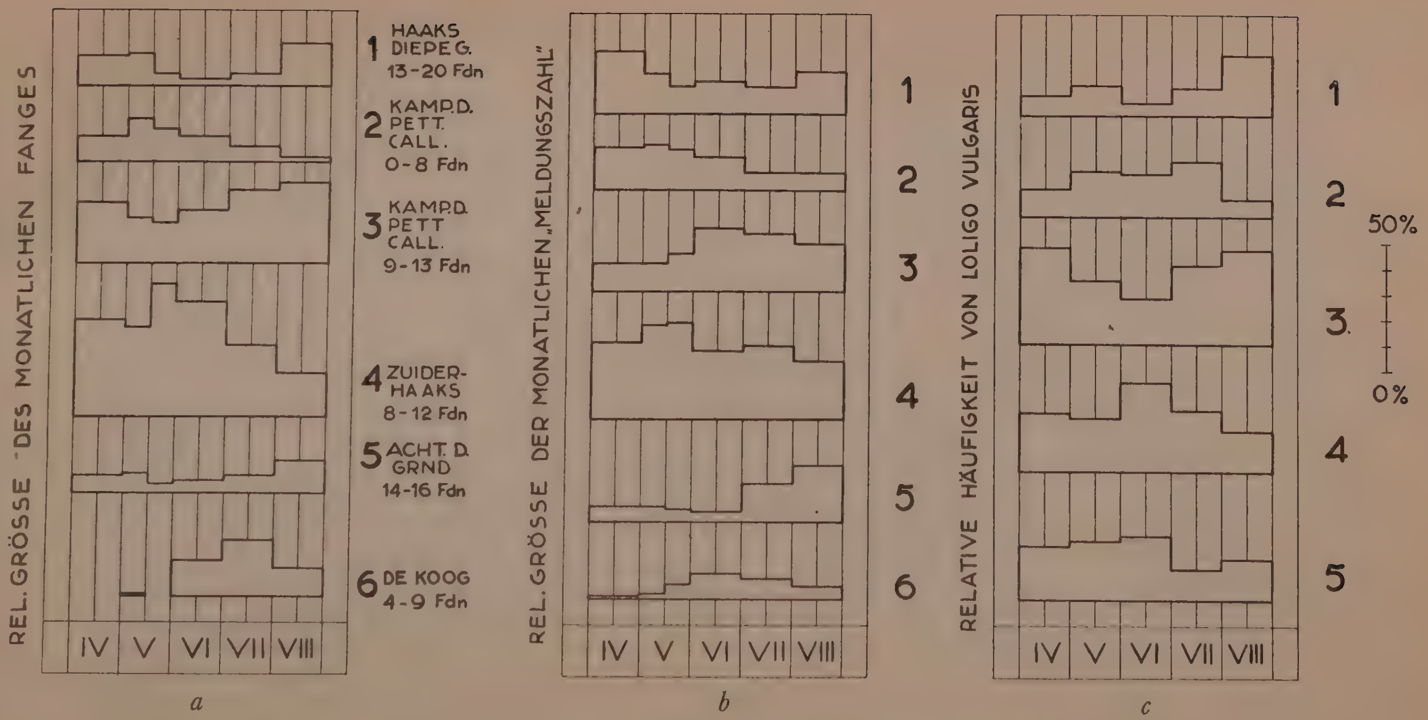

Abb. 15. *a* Fangzahlen; *b*. Intensität der Fischerei; *c*. aus *a* und *b* berechnete Häufigkeit der Kalmare. Durchschnittswerte 1933–1940. Für Einzelheiten siehe den Text.

Quotienten ausdrücken. Diese Prozentsätze sind in Abb. 15c dargestellt. Sie zeigen uns wie ein bestimmtes Gebiet im Laufe des Jahres bald mehr, bald weniger bei den Kalmaren beliebt ist, sagen aber über die absolute Häufigkeit der Tiere sowie über deren Dichte nichts aus. Bei diesen Berechnungen konnte Gebiet No. 6 nicht berücksichtigt werden, da hier zu bestimmten Zeiten nur sehr wenig gefischt wird. Gleichfalls ist Gebiet No. 7 ausgeschlossen, da hier die Fischerei in ganz anderer Weise ausgeübt wird als in den Gebieten No. 1–6.

Die Methode gestattet uns nicht, detaillierte Schlüsse zu ziehen. Nichtsdestoweniger ist Folgendes deutlich. Gebiet 3 zeigt Maxima am Anfang und am Ende der Saison, ein deutliches Minimum im Juni. Gebiet 1 zeigt ein Maximum am Ende der Saison, offenbar kein oder kein ausgeprägtes am Anfang; est ist somit ungewiss ob es, wie Gebiet 3, ein Minimum im Juni hat. Gebiet 4 hat ein deutliches Maximum im Juni, ein Minimum am Ende der Saison, Gebiet 2 hat niedrigere Werte am Anfang und besonders am Ende als in der Mitte der Zeit des Vorkommens. Diese Tatsachen besagen Folgendes. Im Gebiete 3 sind die Tiere relativ häufig am Anfang der Saison, am wenigsten häufig im Juni. Da für das benachbarte Gebiet 2 gerade das Umgekehrte gilt, findet offenbar eine Verschiebung von Tieren von Gebiet 3 nach dem Gebiet 2 statt. Auch im Gebiet 4 aber gibt es eine deutliche relative Zuname, besonders im Juni. Die Verschiebung findet also offenbar vom Gebiet 3 sowohl nach den Gebieten 2 wie 4 statt. Die Kalmare ziehen also mehr oder weniger nach der Küste und zugleich dem Marsdiep zu. Die relative Abnahme in den Gebieten 2 und 4 und die relative Zunahme in den Gebieten 1 und 3 in den Monaten Juli und August zeigt genau das Umgekehrte: eine Verschiebung von der Küste, aber auch vom Marsdiep fort, nach draussen. Global gesprochen nimmt die Tiefe mit der Entfernung von der Küste regelmässig zu (man achte besonders auf die Tiefenlinien der Figur 14 und nicht zu viel auf die Tiefenangaben der Figur 15a). Da die Tiere mit Schleppnetzen unmittelbar am Boden gefangen werden, können wir also sagen, dass sie sich im Juni im Durchschnitt in weniger tiefem Wasser aufhalten als zu Anfang und besonders zu Ende der Saison. Die Tiefe ist dabei aber gewiss nicht das wichtigste Moment, im Gegenteil. Denn die Tiere verbringen den Juni in grosser Anzahl im Gebiet 4, wo die Wassertiefe zum Teil genau so gross ist wie im Gebiet 3. Unten wird sich denn auch zeigen, dass sie an erster Stelle von einem anderen Faktor geleitet werden, nämlich von der Temperatur.

Die Kalmare führen also offenbar innerhalb ihres Sommergebietes ähnliche Bewegungen aus wie z.B. die Schollen. Während aber die Scholle bereits im Mai die wärmsten Stellen besucht, tut dies der Kalmar erst im Juni. Dabei wird die Scholle aber wahrscheinlich hauptsächlich von der Wassertiefe geleitet, der Kalmar von der Temperatur.

Die wenigen Wintertiere, die wir empfingen, kamen im Durchschnitt aus bedeutend tieferem Wasser als die Sommertiere. Wir erwähnten schon, dass einige von diesen in grösserer Entfernung von der Küste als irgendein Sommertier gefangen wurden (S. 251). Auch aus der Verteilung der übrigen Winterfänge geht hervor, dass die Tiere im Winter weiter von der Küste entfernt und in grösseren Tiefen leben. Tabelle 6 gibt die diesbezüglichen Daten. (Diese Wintertiere sind 4–6 Monate alte Stücke, vergl. S. 218.)

TABELLE 6

Gebietswahl bei Den Helder im Sommer und im Winter

	küstenferne Gebiete	küstennahe Gebiete						
		No. 1	3	5	No. 2	4	6	7
Sommertiere (Apr.–Sept.)	180 = 1½%	824	2085	650	1062	4167	661	1677
Wintertiere (Okt.–März)	14 = 25%	27	12	—	—	—	—	2

Bis jetzt betrachteten wir die Ereignisse im „Durchschnittsjahr". Wir werden nun die Verbreitung in den einzelnen Jahren einer näheren Untersuchung unterziehen. Dabei können wir nicht, wie auf S. 251, die Häufigkeit der Tiere berechnen, denn die Intensität der Fischerei kann nicht für jedes Jahr gesondert zahlenmässig dargestellt werden. Wir begnügen uns deshalb mit den Fangziffern. Diese zeigen in den regelmässig befischten Gebieten No. 1–7 erhebliche Schwankungen. Am grössten sind letztere im Wattengebiet (No. 7), wo bald grosse Mengen, bald fast keine Kalmare erbeutet wurden [1]). Anscheinend entspricht dieses Gebiet nur unter bestimmten Umständen den Ansprüchen der Tiere. Welche diese Umstände sind, konnte einigermassen analysiert werden.

Zu diesem Zweck wurde zuerst der Zusammenhang der Kal-

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[1]) Natürlich werden nur diejenigen Monate berücksichtigt, in denen die Wattenfischerei ausgeübt wurde, d.h. April, Mai und Juni (ausgenommen Juni 1938 und 1939, wo keine Beobachtungen gemacht wurden).

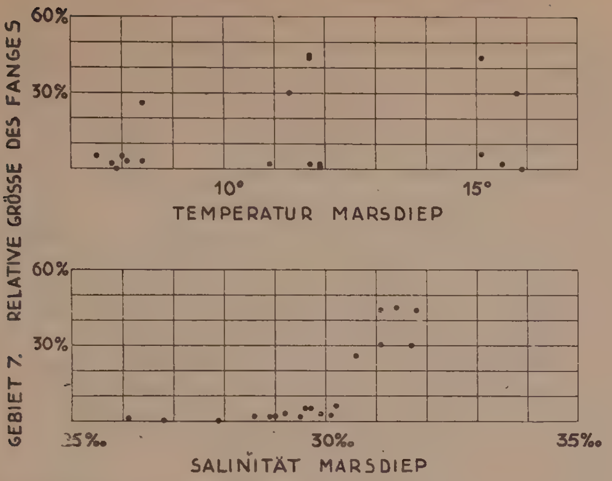

Abb. 16. Beziehungen zwischen Temperatur, Salzgehalt und der relativen Grösse des Fanges im Wattengebiet.

marfänge mit Temperatur und Salzgehalt untersucht. Abb. 16 stellt die Fänge im Wattengebiet (No. 7, Abb. 14), ausgedrückt in Prozenten des monatlichen Gesamtfanges, als Funktion der monatlichen Durchschnittswerte von Salzgehalt und Temperatur im Marsdiep (Westgrenze des Gebietes No. 7; vergl. Abb. 14) dar. Diese Werte sind aus täglichen Oberflächenbeobachtungen am Marsdiepdeich, die Herr Ir. F. Liebert (Rijksinstituut voor Visscherijonderzoek, Den Helder) uns freundlichst zur Verfügung stellte, berechnet worden.

Der Einfluss des Salzgehalts ist sehr ausgeprägt. Nur wenn der Salzgehalt am Deich über etwa $30.3\,^{\circ}/_{\circ\circ}$ steigt, überschreiten die Tiere die Aussengrenze des Wattenmeeres nach innen zu. Weil die Wasseruntersuchung eben am Eingang seewärts des Gebietes No. 7 vorgenommen wurde, können wir folgern, dass eine Salinität von $30.3\,^{\circ}/_{\circ\circ}$ tatsächlich ungefähr die untere Grenze für *Loligo* bildet. Die Temperatur scheint die Tiere gar nicht zu leiten; die Beobachtungspunkte lassen wenigstens nicht auf eine Korrelation schliessen. Dies gilt aber nur für den Temperaturbereich unsrer Beobachtungen und lässt sich nicht ohne Weiteres verallgemeinern.

Von scheveninger Fischern erfuhr P. Creutzberg im Jahre 1941, dass *Loligo vulgaris* querab Scheveningen im Allgemeinen ausserhalb der 3 Meilszone häufiger gefangen wird als in Küstennähe. Dies verwunderte uns anfangs, ist aber nach dem Vorhergehenden leicht verständlich, da die $30^{\circ}/_{\circ\circ}$-Linie sowie mehrere der sonstigen Isohalinen bei Den Helder näher am Strande verlaufen als bei Scheveningen (Atlas, Cons. Int., 1933).

Aus der Feststellung dieser Korrelation zwischen Vorkommen und Salzgehalt können wir jedoch noch keine Schlüsse auf den „Mechanismus" des Zusammenhanges ziehen. Uns kommt es am wahrscheinlichsten vor, dass sich die Tiere unmittelbar auf den Salzgehalt (oder eine seiner chemischen Begleiterscheinungen) orientieren, indem sie sich phobisch von zu süssen Stellen abwenden. Man könnte sich aber auch vorstellen, dass der Zusammenhang indirekt wäre und dass die Kalmare z.B. irgend einem Nahrungstier nachstellen, das sich seinerseits auf den Salzgehalt orientiert. Zur endgültigen Entscheidung dieser Frage fehlen die Beobachtungen; wir haben jedoch keine Anweisungen, dass die letztere, komplizierte Möglichkeit zutrifft.

Die Schwankungen in der Lage der Innengrenze des von Kalmaren besuchten Gebietes werden bei Den Helder also vom Salzgehalt bestimmt. Die Frage drängt sich auf, ob auch die Lage der Aussengrenze Zusammenhänge mit den Schwankungen des „Unterwasserklimas" aufweist. Wir untersuchten deshalb in der obenerwähnten Weise die Korrelation zwischen Umweltfaktoren und dem Vorkommen in den entfernteren Gebietsteilen. Zu diesem Zweck wurde für jeden Beobachtungsmonat der Salzgehalts- und Temperaturdurchschnittswert vom Haaks-Feuerschiff mit der relativen Grösse des Fanges in den Gebieten No. 1, 3, 5 (ausgedrückt in Prozenten des Gesamtfanges in Gebiet No. 1–6) verglichen (siehe Abb. 17).

Auch in diesem Falle übt der Salzgehalt einen Einfluss aus (Abb. 17a). Die Tiere sind nämlich in den entfernteren Gebietsteilen am häufigsten wenn der Salzgehalt beim Haaks-Feuerschiff relativ niedrig, unter $34\,^{\circ}/_{00}$, ist. Jedoch ist der Zusammenhang mit dem Salzgehalt nicht so ausgeprägt wie im Wattenmeer.

Wir sahen oben, dass die Kalmare innerhalb des Küstengebietes jahreszeitliche Wanderungen ausführen. Es lag auf der Hand zu untersuchen, ob die Abhängigkeit vom Salzgehalt noch merkbar ist bzw. besser hervortritt, wenn man den Einfluss dieser Saisonwanderungen eliminiert.

Die relative Häufigkeit der Tiere in Gebiet No. 1, 3 und 5 beträgt nach den Daten aus Abb. 15c für April 67%, Mai 61%, Juni 48%, Juli 54%, und August 77%. Zur Beantwortung unsrer Frage multiplizierten wir die Monatsziffern (Fangzahlen in % des Gesamtfanges in Gebiet 1–6) mit $\frac{48}{67}$ für April, $\frac{48}{61}$ für Mai, $\frac{48}{48}$ für Juni, $\frac{48}{54}$ für Juli, $\frac{48}{77}$ für August und erhielten so eine, sei es

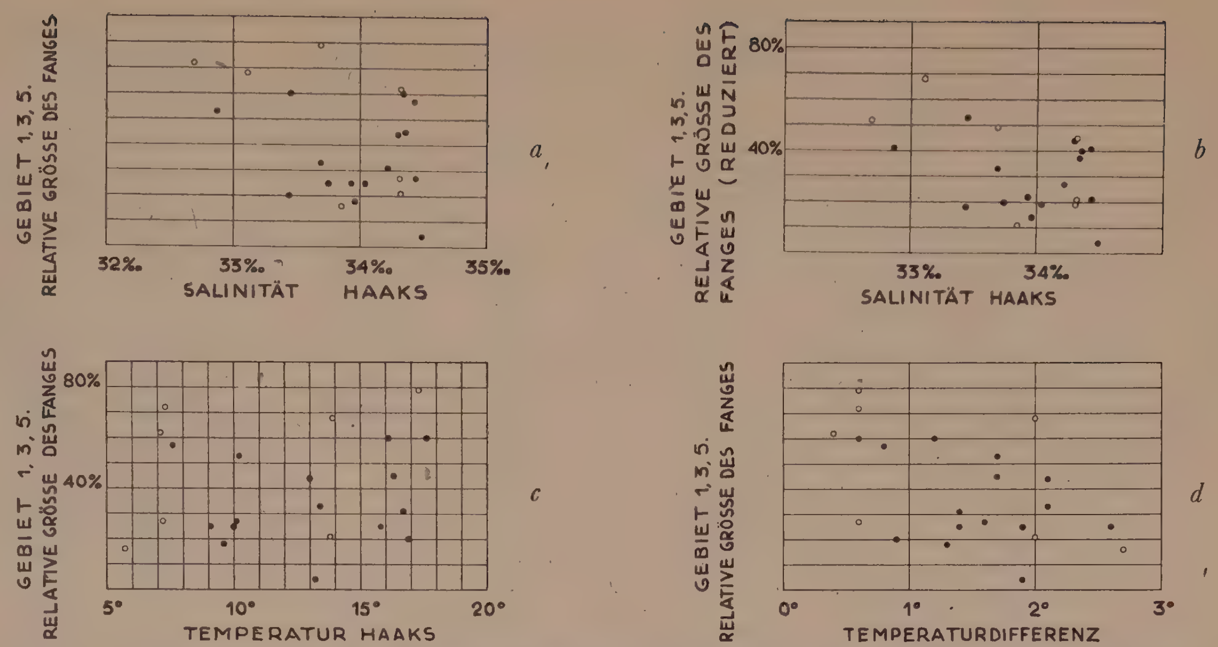

Abb. 17 *a–d*. Beziehungen zwischen der Grösse des Fanges in den tieferen Teilen des Küstenmeeres (ausgedruckt in % des Fanges in den Gebieten 1–6) und dem „Unterwasserklima". ○ Beobachtungen aus Monaten, wo der Gesamtfang 70–200 Stück betrug, ● Beobachtingen aus Monaten, wo dieser über 200 Stück betrug. In Abb. 17*b* ist eine Reduktion angewandt, die im Text erläutert wird; in Abb. 17*d* bedeutet „Temperaturdifferenz" $t_{Marsdiep} - t_{Haaks}$.

auch nur annähernde „Reduktion auf Juniwerte" in arbiträren Einheiten. Die so berechneten Zahlen sind in Abb. 17b als Funktion des Salzgehaltes beim Haaks-Feuerschiff dargestellt. Der Zusammenhang ist wieder sichtbar.

Die Korrelation kann in zwei Weisen gedeutet werden. Man kann annehmen, dass die Tiere von Wasser mit einem Salzgehalt von mehr als 34°/₀₀ abgeschreckt werden. Es ist aber auch möglich, dass der Einfluss vom Salzgehalt in den entfernteren Gebietsteilen nur ein indirekter ist. So könnte man sich vorstellen dass sich die Tiere, von irgendwelchem anderen Faktor geleitet, der Küste zu nähern versuchen, bis sie ihre Salzgehaltsgrenze von etwa 30°/₀₀ erreichen. In süsseren Monaten, wenn diese weit im Meere liegt, würden sie sich dann in grösserer Entfernung von der Küste aufhalten als in Monaten mit höherem Salzgehalt. Die Lage der Aussengrenze ihres Areals würde dann von derjenigen ihrer unteren Salzgehaltsschwelle bestimmt werden und – in unserem Falle – mit dem Salzgehalt im Marsdiep zusammenhängen. Da der Salzgehalt am Haaks-Feuerschiff in grossen Zügen den selben Verlauf hat wie der im Marsdiep, kann man auch nach letzterer Deutung grosse Fänge in Geb. 1, 3 und 5 erwarten bei geringem Salzgehalt am Haaks-Feuerschiff und umgekehrt.

Wir haben aber Anweisungen, dass die zweite Möglichkeit nicht zutrifft. April und Juni 1935 gab es nämlich zugleicherzeit hohen Salzgehalt beim Haaksfeuerschiff und niedrigen Salzgehalt im Marsdiep, wobei die Fänge sowohl in den Gebieten 1, 3 und 5 wie im Gebiet 7 niedrig waren.

	Rel. Grösse des Fanges in Geb. 1, 3, 5	Sal. Haaks	Sal. Marsdiep	Rel. Grösse des Fanges in Geb. 7
April 1935	27%	34.41°/₀₀	28.9°/₀₀	2%
Juni 1935	4%	34.49°/₀₀	30.2°/₀₀	6%

Die Annahme liegt auf der Hand, dass die Tiere im Marsdiep seewärts, beim Haaksfeuerschiff aber nach der Küste hinzu gedrängt wurden. Es blieb also nur eine schmale Zwischenzone (Gebiete 2, 4 und 6) für sie übrig, die im April 71%, im Juni 1935 90% aller angebrachten Tiere lieferte.

Wir halten es deshalb für wahrscheinlich, dass der Salzgehaltseinfluss an den entfernteren Gebieten ein direkter ist und dass die Tiere eine Abneigung gegen Wasser von mehr als 34 ‰ Salzgehalt haben.

Von den weiteren Umweltfaktoren scheint der absolute Wert der Temperatur die Tiere nicht zu beeinflussen (Abb. 17c). Hieraus geht aber noch nicht hervor, dass die Wassertemperatur gar keinen Einfluss ausübt. Und zwar scheinen Zusammenhänge zwischen dem Vorkommen der Kalmare in den Gebieten 1, 3 und 5 und dem Temperaturgefälle im Küstenmeer zu bestehen. Von Februar bis September sind nämlich die küstenferneren Gebiete kälter als die küstennahen. Es scheint nun, dass die Tiere in den Monaten, wo diese Differenz gering ist, am häufigsten sind in den küstenferneren Gebieten. Abb. 17d gibt die diesbezüglichen Monatszahlen als Funktion der Differenz $t_{\text{Marsdiep}} - t_{\text{Haaks}}$. Der Zusammenhang ist ziemlich klar.

Die Temperaturdifferenz zwischen küstenferneren und küstennäheren Gebieten unterliegt einer ausgeprägten jahreszeitlichen Periodizität. Während der uns interessierenden Sommermonate ist sie am grössten im Juni, am geringsten im April und im August. Wir sahen S. 253 (Abb. 15c) schon, dass auch das örtliche Vorkommen der Kalmare eine jahreszeitliche Periodizität zeigt. Tabelle 7 vergleicht die Häufigkeit der Kalmare in den küstenferneren Gebieten, die Grösse des Temperaturgefälles und den Wert des Salzgehalts in Monatsdurchschnittszahlen. Es zeigt sich, dass auch die jahreszeitlichen Wanderungen vom Temperaturgefälle bedingt werden, während der Salzgehalt keinen Einfluss ausübt. Das stimmt, denn in Wirklichkeit haben wir in der Tab. 7 den schon in Abb. 17d nachgewiesenen Zusammenhang nur in etwas anderer Form dargestellt.

TABELLE 7

Vorkommen in den küstenferneren Gebieten und Umweltfaktoren

	Monat				
	IV.	V.	VI.	VII.	VIII.
Relative Häufigkeit in den küstenferneren Gebieten No. 1, 3, 5 (1933–1937). Nach Abb. 15c.	67%	61%	48%	54%	77%
Differenz $t_{\text{Marsdiep}} - t_{\text{Haaks}}$ (1933–'37)	1.0°	1.8°	2.0°	1.3°	0.5°
Salinität Haaks (1933–1937)	33.92	33.81	33.98	33.88	34.06

Wir stellen uns den Zusammenhang mit der Temperaturdifferenz so vor, dass die Tiere eine Vorliebe für die wärmeren Gebietsteile haben. Diese Vorliebe muss bei unseren Beobachtungen desto deutlicher hervortreten, je grösser die Temperaturdifferenz zwischen Küsten- und Haakswasser ist. Es ist weiter klar, dass eine solche Vorliebe die Tiere im Sommer ans Küstenmeer bindet, weil es hier dann wärmer ist als auf hoher See, und gegen den Winter von der Küste vertreibt (vgl. S. 254).

Ein letzter Faktor, der bei der Bindung ans Küstenmeer eine Rolle spielt, ist die Wassertiefe. Wir sahen schon, dass die Tiere, wenigstens im Sommer, nur untiefe Stellen bewohnen. Das Vorkommen hängt also mit der Wassertiefe zusammen. Wenigstens zum Teil ist dieser Zusammenhang ein indirekter, denn Salzgehalt und Temperaturgefälle, die das Vorkommen der Tiere leiten, hängen ihrerseits schon mit der Wassertiefe zusammen. Die Frage drängt sich aber auf, ob die Wassertiefe auch einen direkten Einfluss, unabhängig von der Temperatur und vom Salzgehalt, ausüben kann. Bei unseren Beobachtungen scheint ein solcher Einfluss keine Rolle zu spielen. Im Diepe Gat werden nämlich viele Kalmare erbeutet, während die Wassertiefe hier gleich gross ist wie in den doppelt so weit von der Küste entfernten Gebieten, wo die Art nur selten vorkommt. Dies Alles schliesst die Möglichkeit nicht aus, dass der Tiefenfaktor in Gegenden, wo die Tiefenunterschiede erheblicher als in der Nordsee sind, wohl einen direkten Einfluss ausübt.

Wir wollen noch einmal zusammenfassen, was sich über den Einfluss einiger Umweltfaktoren auf das Vorkommen der Kalmare feststellen liess. Das von den Tieren bevorzugte Gebiet wird bei Den Helder an der Landseite vom Salzgehalt bestimmt, der nicht viel unter ungefähr 30.3°/₀₀ herabsinken darf. An der Meeresseite zeigt die Grenze Zusammenhänge mit dem Salzgehalt und dem Temperaturgefälle im Küstenmeer. Einerseits scheint die Salzgehaltslinie von etwa 34°/₀₀ eine Aussenschranke für die Tiere zu bilden, andrerseits bevorzugen die Tiere das Küstenwasser wegen seiner grösseren Wärme. Die Wassertiefe schliesslich scheint bei der Bindung ans Küstengebiet höchstens eine untergeordnete Rolle zu spielen.

Natürlich sind Salzgehalt und Temperaturgefälle nicht die einzigen Umweltfaktoren die das Vorkommen der Kalmare bedingen. In der Umgebung von Den Helder ist aber deren Einfluss am meisten ausgeprägt. In andersbeschaffenen Gegenden kann die Wirkung dieses oder jenes anderen Faktors deutlicher hervortreten. So erwähnt Lo Bianco (1909) einen Einfluss der Bodenbeschaffenheit: bei Neapel soll die Art eine Vorliebe für schlammigen Grund haben.

Es ist klar, dass die hier gegebene Beschreibung von Korrelationen nur eine Vorstufe in der Erforschung der Orientierung von *Loligo* bildet und keine Schlüsse auf die Art ihrer Reaktionen erlaubt. Da das Verhalten der Tiere im Meere sich unseren direkten Beobachtungen entzieht, wird eine nähere Untersuchung sich wohl auf experimentelle Methoden beschränken müssen und daher schwer ausführbar sein.

b. Das Vorkommen von ♂♂ und ♀♀ gesondert

Die beiden Geschlechter zeigen bei ihrer Gebietswahl einen geringen Unterschied. An den küstenferneren Stationen werden verhältnismässig weniger ♂♂ erbeutet als in der Nähe des Landes. Tabelle 8 gibt die genauen Zahlen.

TABELLE 8

Das Geschlechtsverhältnis an verschiedenen Fundorten

	♂♂	♀♀	Auf 100 ♀♀ fallen:
Gebietsteil No. 1	448	376	119 ♂♂
No. 6	368	293	126 „
No. 5	355	295	131 „
No. 4	2361	1806	131 „
No. 3	1218	867	140 „
No. 2	642	420	153 „
No. 7	1045	632	165 „

Fragt man wieder, welche Umweltfaktoren hier regulierend auftreten, so scheint uns ein direkter Einfluss der Wassertiefe ausschaltbar. Sonst würden die Werte der Gebiete 1 und 7 nicht derart verschieden sein. Anscheinend spielt hier eine der Wassereigenschaften eine Rolle. Man könnte an den Salzgehalt denken, auch aber an die Temperatur. In ersterem Falle würden die ♂♂ einen etwas niedrigeren Salzgehalt bevorzugen als die ♀♀; im letzteren eine etwas höhere Temperatur. Bei Betrachtung der Unterschiede zwischen den Gebieten 2 und 3 einerseits und 5 und 6 andrerseits bedenke man, dass das süssere und (im Sommer) wärmere Wattenwasser bei seiner Ausströmung aus dem Marsdiep in die Nordsee hinein südwärts abgeleitet wird (Ebbe).

Deshalb werden die südlichen Stationen mehr unter Watteneinfluss stehen als die nördlichen, zumal die nördlich von Texel liegende, gleichfalls südwärts ableitende Rinne (das Eyerlandse Gat) in dem Wasserhaushalt der Watten nur eine untergeordnete Rolle spielt. Die jetzt anwesenden Daten erlauben keine weitere Analyse dieser Zusammenhänge.

c. Das Vorkommen der Eier

Die Eiertrauben wurden nur gelegentlich (vor Allem im Jahre 1934) von der Zoologischen Station gekauft; wir haben daher verhältnismässig wenige Fundangaben zu unserer Verfügung. Diese rühren nur vom Küstengebiet her; Tabelle 9 gibt eine Übersicht ihrer Verbreitung für 1934. Zur Vergleichung sind auch die Zahlen der gefangenen Kalmare angegeben.

TABELLE 9

Vorkommen von Eiertrauben und Kalmaren bei Den Helder im Sommer 1934

	Zahl der Eiertrauben	Zahl der Kalmare
Gebiet No. 1	3	37 = 3%
3	24	288 = 20%
5	1	19 = 1%
2	42	170 = 12%
4	20	349 = 24%
6	11	26 = 2%
7	0	554 = 38%
Summe	101	1443 = 100%

Man könnte aus der Tabelle schliessen, dass die Gebiete No. 2 und 6 als Laichort sehr beliebt sind, No. 7 aber abgelehnt wird. Einige Vorsicht ist aber geboten, da die Anzahl nicht gross ist. Wir wagen es darum nicht, diese Daten für eine weitere Analyse zu verwenden.

7. DER GEOGRAPHISCHE VERLAUF DER WANDERUNGEN

In diesem Abschnitt wollen wir versuchen, aus den verfügbaren Literaturdaten und unseren eigenen Beobachtungen den geographischen Verlauf der Wanderungen von *Loligo vulgaris* zu rekonstruieren.

Das Verbreitungsgebiet von *Loligo vulgaris* umfasst das Littoral des Mittelmeeres und der Ostatlantik zwischen 21° und 59° N. [1]). Im atlantischen Gebiet ist die Art an den Küsten NW-Afrikas (ROBSON 1926, BOONE 1933, ADAM 1937*b*, 1941), Portugalls (NOBRE 1932), Frankreichs (LOCARD 1886, DAUTZENBERG und FISCHER 1925, CUÉNOT 1927), Grossbritanniens (Plymouth Marine Fauna 1931, STORROW 1932, MOORE 1937), Belgiens (ADAM 1933), Hollands (TESCH 1908, dieser Beitrag), in der Deutschen Bucht, im Skagerrak und im Kattegat (GRIMPE 1925), in der westlichen Ostsee (GRIMPE 1925, JAECKEL 1937) und schliesslich vielleicht an der norwegischen Küste (GRIEG 1933) festgestellt worden. Im Mittelmeer wird sie u.a. an der französischen (VÉRANY 1853, LOCARD 1886), westitalienischen (JATTA 1896, LO BIANCO 1909) und der tunesischen (GRUVEL 1926) Küste gefunden.

Was die Wanderungen anbelangt, so scheint der Kalmar im Mittelmeergebiet im Winter nicht abzuziehen. VÉRANY (1853) erwähnt für die Umgebung von Nizza: „habite sédentaire les profondeurs moyens". LO BIANCO (1909) nennt die Art für Neapel während aller Jahreszeiten. In den Marktziffern Tunesiens kommen „Calmars" das ganze Jahr hindurch vor, siehe Tabelle 10; aus den Mitteilungen GRUVELS (1926) wissen wir, dass es sich in diesem Falle um unsre Art handelt. In dieser Hinsicht unterscheiden sich also die Kalmare des mediterranen Gebietes erheblich von denjenigen der Nordsee, die wir als ausgeprägte Wandertiere kennen gelernt haben.

TABELLE 10

Marktanlandungen in Tunesien

Summe der Jahre 1932–'36. Nach Bulletin Stat. Océan. de Salammbô No. 31, 33, 35, 36, 37

Monat	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.
kg Kalmare	5327	4626	4849	9148	13137	8792	4466	3973	5181	7916	6391	4170

Es folgt jetzt eine nähere Beschreibung der Wanderungen im Nordseegebiet, dem einzigen Gebiete, von dem Daten in einigermassen genügender Menge vorliegen. GRIMPE (1925) fasste die Angaben über das Vorkommen in diesem Meeresteil schon teilweise zusammen. Sie werden durch unsre Beobachtungen vervollständigt.

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[1]) ADAM (1937a) gibt 2 Stücke für Westindien an, zweifelt aber an der Richtigkeit der Fundortsmeldung.

Loligo vulgaris erscheint, wie wir schon sahen, jährlich in grosser Zahl an der holländischen Küste und erreicht die Umgebung von Den Helder in der zweiten Aprilhälfte. Ihre Anzahl nimmt bis zur zweiten Maihälfte zu und dann wieder rasch ab. Zwischen Ende Juli und Anfang September verschwinden meistens die letzten Stücke. Ihr Alter beträgt rd. 1 und rd. 2 Jahre. Ausserdem werden bei Den Helder im Spätherbst dann und wann kleine Mengen von im selben Jahre geborenen Tieren gefunden. (Im ersten Herbst sind die Bewegungen der Jungtiere übrigens schwer erfassbar, da letztere in Bezug auf die Maschenbreite der üblichen Schleppnetze noch sehr klein sind).

Um die Zugrichtung an der holländischen Küste festzustellen, wurden im Frühling 1937 zu gleicher Zeit in Den Helder und in Breskens (Prov. Zeeland) Kalmare eingekauft. Im letztgenannten Ort konnte dies durch das freundliche Entgegenkommen des Herrn C. L. TER MEULEN stattfinden.

Die hier gelieferten Tiere kamen einerseits von der Scheldemündung und andrerseits von der Nordsee vor den Inseln Schouwen und Goeree. Tabelle 11 zeigt die Zahlen eingekaufter Tiere. In Den Helder kommen die Tiere etwas später als in Breskens an; wahrscheinlich beträgt die Differenz 5–10 Tage [1]).

Kann man hieraus folgern dass die Kalmare von Süden nach Norden ziehen? Streng genommen nicht, denn man könnte sich z.B. auch vorstellen, dass die Tiere quer zur Küste vom tiefen zum seichten Wasser wanderten und diesen Aufstieg im Norden nur etwas später als im Süden unternähmen. In diesem Fall müssten aber vor dem Erscheinen an der Küste Tiere aus tieferem Wasser gemeldet sein. Da letzteres nicht der Fall ist, nehmen wir an, dass die Kalmare parallel zur holländischen Küste nach dem Norden ziehen. Dieses Ergebnis stimmt zu der Annahme GRIMPES (1925), dass *Loligo vulgaris* die südliche Nordsee vom Süden her erreicht, überein.

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[1]) Bei Breskens werden am 14. und 15. April 27 Stück gefangen, bei Den Helder am 19. und 20. April 10 Stück und kurz darauf beträchtliche Mengen. Das gäbe einen Unterschied von ungefähr 5 Tagen. Bei Den Helder sind die Tiere später in der Jahreszeit aber viel häufiger als bei Breskens. Wenn bei Breskens also am 14. und 15. April 27 Stück gefangen werden, sind die Tiere da wahrscheinlich relativ viel häufiger als am 20. April bei Den Helder. Die Differenz beträgt also wohl mehr als 5 Tage, aber wieviel mehr lässt sich nicht entscheiden. Sicherheitshalber nehmen wir an: 5–10 Tage.

TABELLE 11

Frühlingseinwanderung längs der holländischen Küste

Zahlen der 1937 in Breskens (prov. Zeeland) und Den Helder angekauften Kalmare

	April					Mai		
Periode	6.–10.	11.–15.	16.–20.	21.–25.	26.–30.	1.–5.	6.–10.	11.–15.
Breskens	0	28	19	0	7	5	22	55
Den Helder	0	1	11	46	27	124	75	215
Periode	4.–8.	9.–13.	14.–18.	19.–23.	24.–28.	29.–3.	4.–8.	9.–13.
Breskens	0	1	28	18	3	7	5	74
Den Helder	0	0	1	40	17	63	163	101

Anmerkung. Wir haben die Beobachtungszeit in zweierlei Weise in 5-tägige Perioden eingeteilt um sicher davon zu sein, dass das Ergebnis nicht von der zufälligen Wahl einer Unterverteilung beeinflusst worden ist.

Aus den obengenannten Beobachtungen kann man folgern, dass die Tiere, wenn sich auch die Differenz der Erscheinungsdaten nicht genau ermitteln liess, die Strecke Zeeland – Den Helder mit viel grösserer Geschwindigkeit zurücklegen als das Wasser, dessen Strömung hier gleichfalls eine nordostwärts gerichtete Resultante hat. Nehmen wir nämlich an, dass die Entfernung Zeeland–Den Helder 100 Seemeilen beträgt, so legt das Wasser (vgl. Verwey (1943), S. 440 und 445–446) diese Strecke in mindestens 18–25 Tagen zurück, *Loligo* dagegen wahrscheinlich in etwa 5–10 Tagen. Die Wasserbewegung nordwärts ist aber die Resultante einer nordwärts und einer südwärts gerichteten Strömung. Nach unveröffentlichten Messungen des Rijkswaterstaat beträgt die Wasserversetzung nordwärts, an der Oberfläche bei IJmuiden (4 km ausserhalb der Küste), durchschnittlich 10.7 km pro Tide oder 21.4 km pro Tag. Der Weg des Wassers südwärts, 0.15 m über dem Boden, beträgt da 3.2 km pro Tide oder 6.4 pro Tag. Die Differenz zwischen beiden ist 15 km oder 8.3 Seemeilen pro Tag. Sollten die Tiere sich also während der Flut im Oberflächenwasser aufhalten und während der Ebbe nahe am Boden, so würden sie im Durchschnitt 8.3 Seemeilen pro Tag zurücklegen. In diesem Falle würde die Entfernung von 100 Seemeilen, wenn die Stromgeschwindigkeit über die ganze Strecke die gleiche wäre, in ungefähr 12 Tagen zurückgelegt werden. Wenn die Tiere also 6 statt 12 Tage brauchen würden um von Zeeland nach Den Helder zu gelangen, hätten sie ungefähr 8 Seemeilen pro Tag schwimmend zurückzulegen. Jedenfalls müssen wir nicht annehmen, dass sie, wie dies bei dem Ortswechsel zahlreicher Plankter im Wasser und vieler Insekten in der Luft (Fränkel 1932) geschieht, passiv transportiert werden.

In scheinbarem Widerspruch zu unserer Annahme eines Nordzuges durch die Doverstrasse steht, dass die Art an der belgischen Küste nur vereinzelt festgestellt wurde (Adam 1933, 1942 in litt. [1])), während sie an der holländischen Küste bei Breskens, Scheveningen (vgl. S. 255) und Den Helder bestimmt allgemein ist. Es ist aber, wie Herr ADAM uns brieflich mitteilt, sehr gut möglich, dass die Art an der belgischen Küste übersehen wurde, wie dies bis 1931 auch an der holländischen Küste geschah. Darum neigen wir immerhin zu der Annahme, dass die Kalmare der niederländischen Küste die Nordsee durch ihren südlichen Eingang erreichen. (An der französischen Kanalküste ist die Art festgestellt worden (LOCARD 1886, was später von GALLIEN (1934 in litt.) [2]) für Wiméreux (Dept. Pas de Calais) bestätigt wurde. Weitere Angaben über Zahlen und Phänologie liegen für die französische Westküste offenbar nicht vor).

Aus der Deutschen Bucht sind nur verhältnismässig wenig Tiere bekannt. GRIMPE zählt die 1925 bekannten auf; mit den von HERTLING (1934 in litt.) hinzugefügten kommen wir zur folgenden Liste (Tabelle 12). Die Mehrzahl dieser Tiere war reif.

TABELLE 12

Funddaten von Kalmaren in der Deutschen Bucht
(53°56′–55°36′ N, 5°17′–7°51′ O)

Nach GRIMPE (1925) und HERTLING (1934 in litt.)

Mai: 25. V. 1920, 28. V. 1920, 28. V. 1920, 3 Stücke „wahrscheinlich V. 1933".
Juni: 8. VI. 1904.
Juli: 1. VII. 1908, 11. VII. 1903.
Aug.: –
Sept.: –
Okt.: 2. X. 1907.
Nov.: 27. XI. 1933, 28. XI. 1932.

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[1] Herr ADAM teilt uns freundlichst mit, dass nach der Erscheinung seiner Arbeit (1933) folgende Stücke im Brüsseler Museum empfangen wurden: 1. VII. 1925, Ostende, Eier; 6. V. 1938, Ostende, Eier; 18. V. 1927, Ostende, 1 ♀; 11. VI. 1929, Ostende, 1 ♀; 4. IX. 1934, Ostende, 3 Jungtiere (vgl. S. 217 dieser Arbeit). Wie an der holländischen Küste laicht die Art also in den belgischen Gewässern und werden dort im Herbste Jungtiere erbeutet.

[2] Die vielen brieflichen Angaben, die wir im Folgenden erwähnen, rühren von einer Umfrage her, die die Zoologische Station 1934 anordnete. Dabei wurde den westeuropäischen marinbiologischen Instituten ein Fragebogen bezüglich des Vorkommens verschiedener Cephalopodenarten in ihrem Forschungsgebiet zugesandt. Wir sind den Leitern dieser Stationen für ihr freundliches Entgegenkommen bei der Beantwortung sehr zu Dank verpflichtet.

Auf. S. 251 sahen wir schon, dass in der Literatur nur sehr wenig Beobachtungen von der holländischen Küste bekannt waren, obgleich die Art hier bestimmt allgemein ist. Wir halten es deshalb für sehr wohl möglich, dass *Loligo vulgaris* auch in der Deutschen Bucht weniger selten vorkommt als man annimmt, durch Mangel an Beobachtungen aber im küstennahen Meere übersehen wurde. Sind doch die meisten von GRIMPE erwähnten Stücke in ziemlich grosser Entfernung von der Küste erbeutet worden, also im Gebiet, wo nach den helderschen Erfahrungen nur ein kleiner Bruchteil der anwesenden Kalmare verbleibt. Andrerseits besteht aber die Möglichkeit, dass die Art in der Deutschen Bucht eine breitere Zone bewohnt als bei Den Helder, da in ersterem Gebiet die 34°/₀₀-Linie in viel grösserer Entfernung von der Küste liegt als in letzterem.

Auch von der dänischen Westküste sind nur wenig Funde bekannt und diese sind meistens nicht datiert. Etwas besser sind wir unterrichtet über Skagerrak und Kattegat. LÖNNBERG (1891) beschreibt einige Tiere, die alle bei der schwedischen Küste zwischen dem Øresund und der norwegischen Grenze erbeutet wurden. Nach Mitteilung Prof. JÄGERSKIÖLDS (1937 in litt.) und Prof. BOCKS (1942 in litt.) sind seit der Erscheinung der Arbeit LÖNNBERGS weder im Göteborger Museum, noch im Naturhistorischen Reichsmuseum (Stockholm) neue Stücke empfangen worden. Die Funddaten, soweit bekannt, lauten: 8. VII. 1860, 3. VIII. 1869, 18. VIII. 1865, 19. VIII. 1872, 5. IX. 1872, (JÄGERSKIÖLD). LÖNNBERG erwähnt noch eine Mitteilung HANSENS, nach der die Art bei Strömstad im Herbste dann und wann gefangen wird. Aus neuerer Zeit haben wir die Angabe Dr. BLEGVADS (1934 in litt.): „My working district is the Kattegat and the Skagerrak. *Loligo vulgaris* is not common there."

Aus der westlichen Ostsee sind nur ganz vereinzelte Beobachtungen bekannt: 24. IX. 1872 1 ♂ (rd. 30 cm ohne Kopfarme, also wahrscheinlich zweijährig), Travemünde (LENZ 1875); Herbst 1930 in der Kieler Bucht viele 4–5 cm grosse Tintenfische von denen zwei (des 26. XI. 1930) als *Loligo vulgaris* bestimmt wurden (JÄCKEL 1937). (Diese Stücke waren wahrscheinlich im selben Jahre geboren, vgl. S. 218 dieser Arbeit).

Ob *Loligo vulgaris* die norwegische Küste erreicht, ist ungewiss. GRIEG (1933) erwähnt nur ein zweifelhaftes Exemplar, das er in seiner Schlussaufzählung nicht mehr berücksichtigt. Dass die Art bei Bergen und Dröbak auch weiter nicht festgestellt wurde, bestätigten uns Prof. BRINKMANN (1934 in litt.) und Dr. BROCH (1934 in litt.).

Von der britischen Ostküste liegen schliesslich nur wenige Angaben vor. Ältere Daten kann man nicht verwenden, da sie vielfach auf Jeffreys (1869) zurückgreifen, der *Loligo vulgaris* und *Loligo forbesi* noch nicht unterschied und alle Kalmare als *Loligo vulgaris* Lam. benannte. So müssen wir z.B. die Beobachtung McIntosh' (1875) aus der Fauna von St. Andrews (p. 89: „*Loligo vulgaris* Lam. The spawn of this species is frequent") ausser Betracht lassen. Als einige positive Notiz finden wir die Mitteilung Storrows (1932), dass *Loligo vulgaris* im August 1932 regelmässig von den Fischern aus North Shields (Tyne-Mündung) angebracht wurde. Einige negative Angaben lassen wir überdies folgen: Stevenson (1935) erwähnt die Art nicht in seiner Liste der Cephalopoden Yorkshires; ebensowenig traf Russell (1922) sie in den schottischen Gewässern (Ausbeute der „Goldseeker") und Hoyle (1902) fand nicht ein Stück im älteren englischen Museummaterial.

So sind die Beobachtungen, die uns bei der Rekonstruktion der Wanderungen im Nordseegebiet zu Dienste stehen, ziemlich dürftig. Jedoch ist Eines klar: je weiter nördlich, desto später im Jahre erscheint *Loligo vulgaris*. Wir sahen oben, dass die Tiere bei der Scheldemündung früher eintreffen als bei Den Helder. Tabelle 13 zeigt, dass ein ähnlicher Unterschied zwischen Den Helder und der Deutschen Bucht sowie zwischen der Deutschen Bucht und den skandinavischen Gewässern besteht.

Das spätere Erscheinungsdatum der schwedischen Tiere war auch Grimpe (1925) bekannt. Dieser Autor ist geneigt anzu-

TABELLE 13

Vorkommen von *Loligo vulgaris* im Laufe des Jahres

Monat	Den Helder (mittlere Fangzahlen pro Monat 1933–'40)	Deutsche Bucht (sämtliche Fänge siehe Tab. 12)	Skagerrak, Kattegat (sämtliche Fänge)
I.	–	–	–
II.	–	–	–
III.	1	–	–
IV.	181	–	–
V.	1294	3 (+ 3?)	–
VI.	506	1	–
VII.	325	2	1
VIII.	122	–	3
IX.	3	–	2
X.	2	1	–
XI.	1	2	–
XII.	3	–	–

nehmen, dass die schwedischen Tiere zu einer anderen Subspezies gehören als die der südlichen Nordsee und deutet in Zusammenhang hiermit ihr spätes Eintreffen in dem Sinne dass sie die Nordsee durch deren nördlichen Eingang erreichen. Er stellt sogar fest: „vor Allem scheint es ganz ausgeschlossen, dass *L. vulgaris* diagonal durch die Nordsee oder auch entlang ihrer Süd- und Ostküste dem Kattegat zuwandert.'' Nun werden wir weiter unten sehen, dass die von Grimpe angenommenen Rassenunterschiede zwischen nördlichen und südlichen Kalmaren nicht bestehen. Zieht man weiter die Abwesenheit von *Loligo*-Fängen in den norwegischen und schottischen Gewässern in Betracht, so kommt man eher zur Annahme, dass die Art gerade entlang der südlichen und südöstlichen Nordseeküste das Kattegat und Umgebung erreicht. Es wird sich in späteren Beiträgen zeigen, dass es auch unter den Fischen einige Arten gibt, die die dänischen Gewässer hauptsächlich oder ausschliesslich durch die südliche Nordsee hindurch erreichen.

Wie ziehen die Kalmare im Herbste wieder ab? *Loligo vulgaris* kommt bei uns bis zum August, in den schwedischen Gewässern bis zum September vor. Man könnte hieraus folgern, dass unsre Tiere im Spätsommer nach Norden abziehen. Dies ist aber kaum wahrscheinlich, da die Art im Norden viel seltener ist als bei uns. Wir vermuten deshalb, dass die Tiere der südlichen Nordsee durch die Doverstrasse abwandern. Welchen Weg die schwedischen Tiere im Herbste wählen ist ganz ungewiss: einerseits machen die phänologischen Daten einen südlich gerichteten Abzug etwas unwahrscheinlich, andrerseits wurde die Art in den schottischen und norwegischen Gewässern gar nicht festgestellt.

Bevor wir nun das Vorkommen im übrigen Verbreitungsgebiet erwähnen, haben wir die Subspeziesfrage näher zu betrachten.

Steenstrup (1856) hat als erster angegeben, dass Stücke aus dänischen Gewässern einen kürzeren Kopf haben als die aus dem Mittelmeer. Er nannte sie *Loligo breviceps*. Grimpe (1925) spricht von *Loligo vulgaris breviceps* und behauptet, dass die Tiere der südlichen Nordsee der Mittelmeerform ähnlich sind. Letztere tauft er *L. vulgaris typica*. Die Form *typica* sollte an den Frühling, die Form *breviceps* an Spätsommer und Herbst gebunden sein. An andrer Stelle in derselben Arbeit erwähnt Grimpe aber die Möglichkeit, dass sich die Unterschiede der beiden Subspezies „einfach als Wachstums- bzw. Altersunterschiede erklärten'' (S. 33).

Trotz diesem Vorbehalt wird auf S. 34 bei seinem No. 2 mitgeteilt: „Aus diesen Massen geht unzweideutig hervor, dass es sich bei diesem ♂ um ein typisches Stück von *L. vulgaris* handelt"; bei No. 3: „dieses ♂ muss ohne Frage der „Subspezies" *breviceps* zugeschrieben werden," bei No. 5: „. . . gehört . . . deutlich zu *L. typica*." und bei No. 6/7: „gehören ebenfalls sicher zur typischen Form."

Als Kriterium bei dieser Unterscheidung verwendet Grimpe die Verhältniszahlen $\frac{\text{ventrale Mantellänge}}{\text{Kopflänge}}$ und $\frac{\text{ventrale Mantellänge}}{\text{Armlänge}}$. Letztere Zahl scheint insoweit nicht zuverlässig, als bei der Fixierung die skelettlosen Arme ungleich schrumpfen können. Wir beachten deshalb nur den Quotienten $\frac{\text{ventrale Mantellänge}}{\text{Kopflänge}}$. Bei Grimpe findet man diesen Wert fur *L. vulgaris typica* als 6.1 und

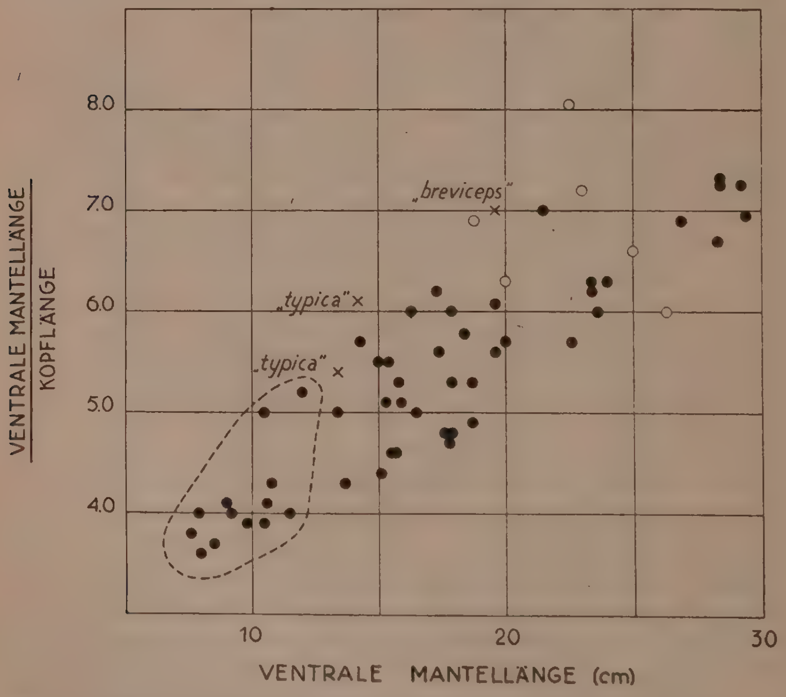

Abb. 18 Zusammenhang von relativer Kopflänge und ventraler Mantellänge bei ♂ Kalmaren. ● (nicht umrandet) 15. – 28. VIII. 1936, Den Helder; ● (umrandet) III., IX., XII., Den Helder; o IV. – VI., Den Helder; × Grimpes (1925) Messungen.

5.4, für *L. v. breviceps* als 7.0 festgestellt. Wo er die Grenze zieht, wird nicht angegeben.

Wir massen in verschiedenen Monaten Kopf- und Mantellängen von bei Den Helder gefangenen Tieren. Dabei zeigte sich, dass der Wert des Quotienten in hohem Masse vom Alter des Tieres abhing. Deshalb sind in Abb. 18 die von uns gefundenen Verhältniszahlen sowie diejenigen GRIMPES als Funktion der Mantellänge dargestellt. Es ist klar, dass die Quotienten nur unter Berücksichtigung des Alters (bzw. der ventralen Mantellänge) verwertet werden können. Es zeigt sich weiter, dass GRIMPES Rassenmerkmale tatsächlich nur vom Alter bedingt werden; sein *L. v. breviceps* könnte sich nach der Graphik der Abbildung 18 sehr wohl aus einem seiner *typica*-Stücke entwickelt haben.

Schliesslich geht aus den Messungen hervor, dass die holländischen Maitiere im Vergleich zu den Augusttieren eher kurzköpfiger als langköpfiger sind und sich übrigens von diesen wahrscheinlich nicht unterscheiden. (Nach GRIMPES Auffassung könnte man erwarten, dass die Maitiere eher einen längeren Kopf hätten, siehe oben).

Es kommt uns deshalb vor, dass wir keinen Grund haben, die *Loligo vulgaris* des Nordseegebietes in zwei Rassen zu spalten, eine Folgerung, die wir S. 269 bei der Behandlung der Zugwege schon verwendet haben. Ob die Nordseetiere morphologische Unterschiede mit den Mittelmeertieren aufweisen, müssen wir durch Mangel an Material dahingestellt sein lassen.

Wir kehren schliesslich zum Vorkommen im übrigen Verbreitungsgebiet zurück. Bezüglich der Zeit des Vorkommens an den atlantischen Küsten NW-Afrikas, Portugalls, Frankreichs und an den französischen und englischen Kanalküsten fanden wir nur die Notizen CUÉNOTS (1927) und die Fischereistatistiken Portugalls. Nach CUÉNOT erscheint *Loligo vulgaris* zwischen Mai und Oktober mit unentwickelten Gonaden in der Baie von Arcachon. Dieses Verhalten weicht erheblich von dem ab, was wir in der Nordsee festgestellt haben. Unentwickelte Geschlechtsdrüsen finden wir bei der Mehrzahl der *Loligo forbesi* Ststrp. an unserer Küste, so dass man sich fragt, ob eine Verwechslung mit dieser Art vorliegen könnte.

Interessant sind die portugiesischen Fischereistatistiken (Estatistica usw. 1929–1939), denen wir die Marktanlandungsziffern für Lissabon entnehmen. In diesen trifft man eine Rubrik „Lulas" an. Nach GIRARD (1889a) und NOBRE (1932) bezieht sich dieser Name auf *Loligo vulgaris* Lam. und *L. media* L. (= *Alloteuthis subulata* Lam.). Aus Girards Ausführungen können wir weiter folgern, dass *L. forbesi* Ststrp. auf dem Markte von Lissabon nicht von *L. vulgaris* unterschieden wird; auch diese Art wird also wahrscheinlich als „Lula" benannt. Trotzdem ist es klar, dass sich die genannten Ziffern an erster Stelle auf *L. vulgaris* beziehen, denn dieser Kalmar ist nach Nobre sehr allgemein auf dem Lissaboner Markte, während *Alloteuthis subulata* nach Girard (1889b, S. 255) „se montre très rarement sur le marché de Lisbonne" und *L. forbesi* vom selben Autor als „rara especie" bezeichnet wird.

Tabelle 14 gibt nun die durchschnittlichen monatlichen Fangziffern für die Jahre 1928–1937; sie werden in Abb. 19 graphisch dargestellt und mit den Zahlen von Tunesien und Den Helder verglichen. Der Fang in Lissabon unterliegt einer auffälligen Periodizität, indem er im Winter (Oktober–März) viel grösser ist als im Sommer. Dies könnte etwa von einer geringen Haltbarkeit der Kalmare während des Sommers hervorgerufen werden; wenn wir aber die Zahlen des viel wärmeren Tunesiens in Betracht ziehen, hat diese Annahme nicht viel Wahrscheinliches. Letztere zeigen nämlich in den Monaten April bis Juni statt einer Abnahme einen stark hervortretenden Gipfel. Wir nehmen deshalb an, dass die Lissaboner Sommerfänge klein sind, weil die Art hier zu dieser Zeit verhältnismässig selten vorkommt.

TABELLE 14

Marktanlandungsziffern für Lissabon

Nach Estatistica das Pescas maritimas (1929–1939). Durchschnittlicher Fang pro Monat, 1928–1938

Monat	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.
Kalmare (in 1000 kg)	9.9	10.2	7.5	3.3	2.7	2.4	1.9	1.6	4.9	8.6	12.6	9.3

Die Abnahme im Frühling muss also durch Abzug verursacht werden. Da die Art im Norden nur im Sommer erscheint, ist es nicht unwahrscheinlich, dass dieser Abzug S–N gerichtet ist. Beweise für diese Annahme könnte man in erster Linie in den französischen Fischereistatistiken finden. Leider behandeln diese aber die Kalmarfänge nicht gesondert.

Es fällt auf, dass das Maximum der Fänge in Tunesien zeitlich zusammenfällt mit demjenigen in der südlichen Nordsee. Dies beeinträchtigt einigermassen

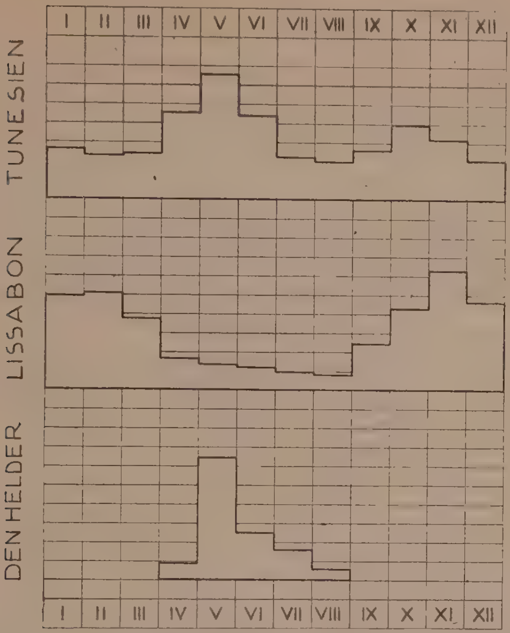

Abb. 19. Durchschnittliche monatliche Fangzahlen für Tunesien (1932–1936; siehe Tabelle 10), Lissabon (1928–1938; siehe Tabelle 14) und Den Helder (1933–1940, siehe Tabelle 13). Skala: Tunesien 1 Teilstrich = 400 kg, Lissabon 1 Teilstrich = 2000 kg, Den Helder 1 Teilstrich = 200 St.

unsre Deutung, nach welcher Lissabon seine Tiere im Sommer an den Norden abgeben würde. Ein Teil könnte ja auch nach Tunesien abwandern. Letztere Möglichkeit können wir in der Tat nicht ausschliessen, wir halten sie aber für sehr unwahrscheinlich.

Weiter interessieren noch einige Daten aus dem äussersten Westen Europas. In irischen Gewässern wurde die Art nach Massy (1909, 1928) nicht festgestellt. Von der britischen Westküste aber liegen einige beachtenswerte Angaben vor. H. B. Moore (1937) gibt nämlich folgende Notiz für Port-Erin (Isle of Man): „Taken frequently in seine nets in Port-Erin Bay and according to local fishermen said to be even more common off shore", letztere Angabe mit der Fussnote: „This record requires verification" (S. 195). Der selbe Autor meldet uns (1934 in litt.): „These squid are present all the year round, showing no apparent seasonal fluctuation, . . . All the above data are obtained from the men, but I have myself verified the identity of the species." Leider fehlen also genauere Einzelheiten. Trotzdem ist das Mitgeteilte von Interesse für unsre weiteren Betrachtungen (siehe S. 276).

Hiermit ist unser Tatsachenmaterial erschöpft. Wir müssen feststellen, dass unsre Einsicht in den Verlauf der Wanderungen von *Loligo vulgaris* noch recht lückenhaft ist. Was bei der Vervollständigung des Bildes vor Allem fehlt, sind genaue phänologische Beobachtungen aus den verschiedenen Teilen des Verbreitungsgebietes. Planmässiger Ankauf von den Fischern ist wohl die einfachste Methode, die zum Ziel führt. Sie kann an einer marinbiologischen Station meistens ohne grossen Aufwand an Geld und Energie ausgeführt werden.

Trotz der Beschränktheit unsrer Kenntnis ist eine vergleichende Besprechung von einigen unsrer Ergebnisse lohnend.

Wir sahen oben, dass *Loligo vulgaris* das Mittelmeer im Winter nicht verlässt, die Nordsee aber wohl.

Gleichartig verhält sich *Sepia officinalis* L. Im Mittelmeer wird die Art das ganze Jahr hindurch gefunden (VÉRANY 1853, JATTA 1896), in der Nordsee ist sie aber nach unseren Beobachtungen stark an den Vorsommer gebunden [1]).

Einen ähnlichen Unterschied im Zugverhalten zeigen mehrere Vogelarten. Bei diesen benehmen sich nicht nur die Populationen Nordeuropas anders als diejenigen aus Südeuropa, sondern auch unterscheiden sich die des kontinentalen Zentral- und Osteuropas von denen des maritimen Westeuropas. Wir können also sagen, dass es einen Zusammenhang gibt zwischen der Strenge des Winters an einem bestimmten Ort und der Bereitschaft der Tiere von dort im Herbste wegzuziehen. Einige Vogelarten seien hier als Beispiel ganz kurz behandelt.

Fringilla coelebs L. (Buchfink). Die skandinavischen, ostbaltischen und mitteldeutschen Brutvögel sind vorwiegend Zugvögel; die italienischen (ARRIGONI DEGLI ODDI 1929) und sardinischen (TOSCHI 1939) Brutvögel sind Standvogel. – Im Ostbaltikum und Mitteldeutschland vorwiegend Zugvogel, in Holland vorwiegend Standvogel. In England und Irland Standvogel (WITHERBY 1938, weitere Buchfinkenliteratur bei TINBERGEN 1941).

Sturnus vulgaris L. (Star). In Skandinavien, im Ostbaltikum und in Südostdeutschland zu einem kleineren oder grösseren Teil wegziehend (SCHÜZ und WEIGOLD 1931). In Nord- und Mittelitalien Standvogel (TOSCHI 1939). – Im Ostbaltikum und Südostdeutschland z.T. wegziehend, in England und Irland Standvogel (WITHERBY 1938).

Unter den weiteren Arten, die im nördlichen Teil ihres Verbreitungsgebietes wegziehen, in Italien aber Standvögel sind, können genannt werden: *Alauda*

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[1]) Im Gegensatz hierzu ist *Loligo forbesi* Ststrp. im Mittelmeer sowie im Nordseegebiet ein Wandertier.

arvensis L., *Lullula arborea* (L.), *Regulus regulus* (L.), *Phylloscopus collybita* (Vieill.), *Sylvia atricapilla* (L.), *Erithacus rubecula* (L.), *Accipiter nisus* (L.), (ARRIGONI DEGLI ODDI 1929, TOSCHI 1939).

Weitere Arten, die im kontinentalen Teil ihres Verbreitungsgebietes wegziehen und im maritimen nicht, sind: *Accipiter nisus* (L.) (in Deutschland oft wegziehend (NIETHAMMER 1937–1938), in Holland selten wegziehend (EYKMAN c.s. 1937, Ringfunde des Leidener Museums), in England Standvogel (WITHERBY 1938)); *Sitta europaea* L. und *Troglodytes troglodytes* (L.) (beide Arten sind in Holland Standvogel (EYKMAN. c.s. 1937), ziehen in Zentralrussland aber öfters weg (GROTE 1940)); *Certhia familiaris* L. (in England Standvogel (WITHERBY 1938), in Zentralrussland wenigstens z.T. wegziehend (GROTE 1940)). Schliesslich erhält man aus den Beschreibungen GROTES den Eindruck, dass die *Parus*-Arten in Zentralrussland verhältnismässig in grösseren Zahlen am Zuge teilnehmen als z.B. in Westeuropa.

Es gibt weiter verschiedene Vogelarten, die sowohl im Norden (bzw. Osten) als im Mittelmeergebiet (bzw. Westen) wegziehen. Wir kennen aber keine Beispiele von Arten, die im Norden überwintern und im Mittelmeergebiet wegziehen.

Was die Verursachung der Unterschiede im Zugverhalten anbelangt, können wir schliessen, dass entweder im Süden für die genannten Arten die Reize zum Wegzug fehlen oder dass die hier wohnenden Tiere gegen dieselben unempfindlich sind. Welche dieser beiden Möglichkeiten für den Wegzug im Herbste zutrifft, können wir nicht entscheiden. Betrachten wir aber den Zug nordwärts im nächsten Frühling, so ist es klar, dass im Süden (bzw. im maritimen Teile des Verbreitungsgebietes) die zugauslösenden Reize anwesend sind, aber dass die hier wohnenden Tiere unempfindlich dagegen sind. Denn die nördlichen Formen verschiedener der eben genannten Arten überwintern gerade im Brutgebiet der südlichen Rassen. Wenn der Frühling anbricht ziehen erstere nach Norden, während letztere an Ort und Stelle bleiben.

Der Effekt der Erscheinung ist schon genannt: dort, wo der Winter streng ist, verschwinden die Tiere; wo er mild ist, bleiben sie. Die im Norden abgezogenen Tiere überwintern ohne Ausnahme an Stellen, wo der Winter milder ist als in ihrem Brutgebiet. Man kann annehmen, dass dies eben notwendig ist, weil sie in ihrem Brutgebiet den Winter nicht überstehen können. Jedoch können wir in dieser Hinsicht nichts beweisen; dazu brauchte man eine Schätzung der Mortalität, welche die Tiere erleiden würden, wenn sie im Winter den Norden nie verliessen – eine komplizierte Aufgabe. Aus den oben erwähnten Tatsachen können wir aber nur schliessen, dass sich die Arten im Süden ohne Zugverhalten instand halten können.

Kehren wir jetzt zu *Loligo vulgaris* zurück. Wir fanden, dass die nördlichen Tiere dieser Art ziehen, die Mittelmeertiere dagegen nicht. Wir können sagen, dass die Mittelmeertiere gegen die zugauslösenden Reize entweder unempfindlich sind oder denselben nicht ausgesetzt werden. Welche dieser beiden Möglichkeiten zutrifft, lässt sich aber nicht entscheiden, da die Reize für die Tiere im Mittelmeer andere sein können als für die Tiere aus dem Norden, die – wie wir S. 272 sahen – den Winter wohl an der atlantischen Südwestküste Europas verbringen.

Wir sahen oben, dass die Kalmare aus dem Gebiet der Nordsee aller Wahrscheinlichkeit nach den Winter – wie die Zugvögel – in wärmeren Gegenden verbringen.

Die Wanderungen haben also den Effekt, dass *Loligo* der Winterkälte und deren Nebenerscheinungen nicht ausgesetzt ist. Inwieweit letzterer Effekt notwendig ist, lässt sich aber nicht angeben (wir sahen schon, dass eine andere Funktion der Wanderungen das Erreichen der Laichgebiete ist, vgl. das S. 244 Bemerkte).

Wir haben festgestellt, dass es Vogelarten gibt, die die maritimen westeuropäischen Gebiete – anscheinend im Zusammenhang mit dem milderen Klima – im Winter nicht verlassen, die östlicher liegenden kontinentalen Gebiete aber wohl. In dieser Beziehung ist das Verhalten der Kalmare im Irischen Meere, das wir S. 274 aus den Beobachtungen Moores kennen lernten, von Interesse. Nach Moore sollten die Tiere hier Sommer und Winter anwesend sein. Tatsächlich ist der Winter im Irischen Meere etwas wärmer als in der Nordsee, wie aus den Mitteilungen Bruces (1928) hervorgeht. Allerdings ist das Minimum der Jahreskurve in Port-Erin nur 1.5 höher als dasselbe beim Haaksfeuerschiff in der Nordsee doch wurden Bruces Beobachtungen „at a point close inshore in one or two fathoms of water" gemacht. Der tatsächliche Unterschied zwischen der Nordsee bei Haaks und dem Irischen Meer unweit Port-Erin wird also etwas grösser sein, da tiefere Stationen im letzteren Gebiet zweifelsohne höhere Wintertemperaturen zeigen werden. -- Es wäre wichtig, genauere Angaben über das Vorkommen von *Loligo vulgaris* bei Port-Erin zu besitzen.

Es erübrigt sich jetzt, den Verlauf des Zuges von *Loligo vulgaris* mit demjenigen anderer Cephalopoden zu vergleichen. Zuerst betrachten wir einige Arten aus dem Nordseegebiete.

Sepia officinalis zeigt grosse Übereinstimmung mit *Loligo vulgaris;* sie kommt in einem anderen Beitrag aber gesondert zur Sprache.

Die Wanderungen von *Alloteuthis subulata* werden von Grimpe (1925) ausführlich beschrieben. Nach diesem Autor erscheint sie Anfang März in der nördlichen Nordsee und verbreitet sich von dort südwärts um z.B. etwa Anfang Mai die Deutsche Bucht zu erreichen. Adàm (1933) hat aber nachgewiesen, dass sie im April schon vor der belgischen Küste vorkommt und erwähnt weiter einen Februarfang von Kap Gris-Nez. Es hat also allen Anschein, dass die Art im Süden und im Norden der Nordsee zu gleicher Zeit erscheint. Grimpe nimmt stützend auf Massys (1909) Beobachtungen an, dass die Nordseetiere im

Oktober westwärts abziehen und den Winter in etwa derselben Breite verbringen als den Sommer. Ob dies auch für die im Frühling die Doverstrasse einziehenden Tiere gilt, müssen wir dahingestellt sein lassen. Es ist aber klar, dass bei *Alloteuthis subulata* ganz andere Verhältnisse vorliegen als bei *Loligo vulgaris*, die im Norden ja erst spät im Jahre erscheint.

Wenn auch weitere Einzelheiten erforderlich sind, können wir doch bemerken, dass diese Verhältnisse an diejenigen, die wir bei einigen Vogelarten Mitteleuropas finden, erinnern. So ziehen die ostbaltischen Stare (*Sturnus vulgaris* L.) und die nordwestdeutschen Saatkrähen (*Corvus frugilegus* L.) im Herbste westlich ab und überwintern in England und Irland, während die russischen Populationen letzterer Art gleichfalls stark westlich abziehen (vgl. z.B. NIETHAMMER 1938). Wie die von GRIMPE angenommenen Winterquartiere von *Alloteuthis subulata* neben ihrer Tiefe dem Einflusse des Golfstromes relativ hohe Wintertemperaturen verdanken, so ist auch das milde Klima im Wintergebiet der genannten Vogelarten letzterem Faktor zuzuschrieben.

Loligo forbesi wird, wie *Sepia officinalis*, in einem gesonderten Beitrag behandelt werden. Die Wanderungen dieser Art findet man, wie die der anderen Nordseecephalopoden, in der Literatur nicht beschrieben.

Einige Angaben über verwandte Arten in anderen Gebieten seien noch herangezogen.

Treffend ist die Übereinstimmung in den Wanderungen von *Loligo vulgaris* und *Loligo pealii*. Über diese amerikanische Art unterrichten uns die Arbeiten VERRILLS und BIGELOWS. Sie ist die gewöhnliche „Squid" der ostamerikanischen Küste zwischen Cape Hatteras und Cape Cod. Im Sommer ist sie an das Littoral gebunden. Im Gulf of Maine erscheint sie im Frühling, laicht den ganzen Sommer hindurch in Tiefen von 0 bis etwa 50 m und verschwindet im Herbst. Im Norden erscheint sie später und verschwindet sie früher als im Süden. Da Fänge aus tieferem Wasser nach BIGELOW fehlen, sind wir geneigt anzunehmen, dass die Art längs der Küste vom Süden her einwandert.

Die morphologischen Unterschiede zwischen *L. pealii* und *L. vulgaris* sind ziemlich gering. Da auch die Biologie der beiden Arten – soweit bekannt – in mancher Hinsicht übereinstimmt, fragt man sich, ob sie nicht als zwei Rassen ein und derselben Art betrachtet werden müssen.

Wanderungen vom Süden nach Norden werden weiter von SASAKI (1921) für *Ommastrephes pacificus sloani* beschrieben, die im Frühling in nordöstlicher Richtung der japanischen Küste folgt.

Wir kennen also mehrere Beispiele von Cephalopodenarten, die wie viele Zugvögel im Frühling in etwa nördlicher Richtung den gemässigsten Gebieten zuwandern. Daneben scheinen aber andere Wanderungstypen vorzukommen.

8. ZUSAMMENFASSUNG

1. Der vorliegende Beitrag, dessen Problemstellung viele Einzelfragen umfasst, gilt der Erforschung der Biologie von *Loligo vulgaris* Lam. Die Arbeit fusst auf der Untersuchung von etwa 12000 in der Nähe von Den Helder erbeuteten Stücken. Die Art kommt in dieser Umgebung vom April bis August allgemein und in den übrigen Monaten vereinzelt vor; sie pflanzt sich hier regelmässig fort.

2. Das Wachstum wurde mittels der Analyse von Frequenzkurven der ventralen Mantellängen festgestellt.

3. Anfang Mai haben die Längenfrequenzkurven der fast ein Jahr alten ♂♂ einen Gipfel bei 13–14 cm und die der fast zwei Jahre alten bei 21 cm, während drei Jahre alte Tiere wahrscheinlich selten vorkommen. Eine schematische Wachstumskurve der ♂♂ gibt Abb. 4.

4. Die ♀♀ wachsen, bis sie eine Länge von etwa 12 cm erreicht haben (d.h. bis sie $\frac{1}{2}$–$\frac{3}{4}$ Jahre alt sind) gleich schnell wie die ♂♂. Im zweiten Lebensjahre wachsen sie erheblich langsamer als die ♂♂, so dass die Gipfel ihrer Frequenzkurven im Monat Mai bei etwa 13–14 cm und etwa 17 cm liegen. Langsames Wachstum im zweiten Lebensjahre ist gleichfalls bei den ♀♀ von *Loligo pealii* Les. und *Sepia officinalis* L. festgestellt worden. Dreijährige ♀♀ von *L. vulgaris* scheinen selten vorzukommen.

5. Die einjährigen Tiere erscheinen durchschnittlich später im Frühling als die zweijährigen. Gleiches finden wir bei vielen zum Fortpflanzungsgebiet ziehenden Fischen und Vögeln.

6. Das Geschlechtverhältnis der Laichzügler ist ungleich; im Gesamtergebnis wurden 57% ♂♂ erbeutet. Durchschnittlich ist der Prozentsatz der ♂♂ anfangs etwas höher als später im Sommer, was aber nicht für jedes einzelne Jahr zutrifft. Die Reihenfolge der Geschlechter auf dem Zuge zum Fortpflanzungsgebiet wird vergleichend besprochen und es werden die Zusammenhänge mit der Paarungsbiologie behandelt.

7. Das Laichen dauert solange die Tiere das Gebiet in grosser Menge besuchen, also vom April bis August. In der 2. Maihälfte, wenn die meisten Tiere anwesend sind, erreicht es seinen Gipfelpunkt.

8. Bei den im selben Jahre geborenen ♂♂ enthält der Hoden schon im Oktober Spermatozoen. Seine Entwicklung geht im Laufe des Winters weiter, erreicht Mai–Juli den Gipfelpunkt um im August wieder abzunehmen. Wie weit sie im zweiten Winter wieder zurückgeht, konnte nicht festgestellt werden. Von den zwei Jahre alten Tieren lässt sich nur sagen, dass der Hoden im Frühling und Vorsommer stark entwickelt ist und dass er sich im August wieder rückbildet.

9. Die im selben Jahre geborenen ♂♂ haben schon im Dezember Spermatophoren im Spermatophorensack. Bis zu ihrem Erscheinen im April übertrifft bei ihnen (sowie bei den zweijährigen ♂♂) die Spermathophorenproduktion den Verbrauch (der dann wohl gleich Null zu setzen ist). Sobald die Tiere eingetroffen sind, übertrifft aber der Verbrauch die Produktion, welche jedoch nicht aufhört. Das Ergebnis ist, dass die Spermatophorensäcke immer leerer werden.

10. Die im selben Jahre geborenen ♀♀ haben im Dezember keine Eier im Ovidukt, während die Eier im Ovar noch sehr klein sind. Akzessorische, Nidimental- und Oviduktdrüsen stehen noch im Anfang ihrer Entwicklung. Zwischen Dezember und April entwickelt sich das Ovar stark; eine Abnahme zu Ende des Sommers konnte nicht festgestellt werden.

11. Vor der Ankunft der Tiere im Laichgebiet häufen sich Eier an im Ovidukt, während noch keine abgelegt werden. Die Ovidukte sind also mehr oder weniger gefüllt. Kurze Zeit nach der Ankunft werden mehr Eier abgelegt als solche an den Ovidukt abgegeben werden, und die Zahl der Tiere mit leeren oder wenig gefüllten Ovidukten nimmt zu. Nach Ende Mai aber halten Verbrauch und Ersatz im Durchschnitt gleichen Schritt. Wahrscheinlich werden die Eier nicht kontinuierlich, sondern in einigen Gelegen abgesetzt.

12. Bei Den Helder setzen die ♂♂ von *Loligo vulgaris* ihre Spermatophoren ausschliesslich auf der Mundmembran des ♀ ab, wo sich die Spermatheca (= das Receptaculum Seminis) findet. Letzteres Organ ist bei der übergrossen Mehrzahl der Sommerweibchen mit Sperma gefüllt. Aus dem Vorkommen frisch abgesetzter Spermatophoren kann man folgern, dass die ♀♀ während des ganzen Sommers begattet werden und zwar im Anfang und zu Ende der Zeit etwas weniger als in der Mitte.

13. Zweijährige Kalmare haben im Verhältnis zu ihrer Grösse einen stärker gefüllten Spermatophorensack bzw. mehr

Eier im Ovidukt als einjährige, was zu Vergleichungen mit Tieren aus anderen Tiergruppen Anlass gibt. Bei den Vögeln kommt öfters vor, dass ältere Weibchen mehr Eier legen als jüngere.

14. Verschiedene Cephalopodenarten haben, wie *Loligo vulgaris*, eine periodische Fortpflanzung. Bei einigen Arten dauert die Laichzeit im Mittelmeer länger als im Nordseegebiet, was auf einen Temperatureinfluss hindeuten könnte.

15. Die Fortpflanzung von *Loligo vulgaris* fängt in der Nordsee bei zunehmender, im Mittelmeer (nach Lo Biancos Angaben) bei abnehmender Tageslänge an, was nicht für einen grossen Einfluss dieses in Zusammenhang mit der Fortpflanzungsperiodizität der Vögel so wichtigen Faktors spricht. Andrerseits ist eine gemeinsame Verursachung von Fortpflanzungs- und Zugperiodizität nicht unwahrscheinlich und werden wir unter 18. sehen, dass letztere wahrscheinlich eben wohl von der Tageslänge beeinflusst wird.

16. Eine der Funktionen des Zuges ist das Erreichen der Laichgebiete. Eine Einteilung der Wanderungstypen nach ihrer Funktion ist nicht angebracht, da meistens mehrere Funktionen zusammengehen.

17. Die Periodizität des Zuges geht hervor aus Abb. 13. Die Auswanderung folgt der Einwanderung unmittelbar, ohne dass ein stationnärer Zustand eintritt.

18. Das Anfangsdatum der Einwanderung zeigt von einem Jahr aufs andere nur eine geringe Streuung, die Zusammenhänge mit der Wassertemperatur zeigt. Die Tiere erscheinen nämlich in kalten Jahren später als in warmen. Der Einfluss der Temperatur ist nur ein untergeordneter; viel wichtiger ist der Faktor „time of year" (Nice), d.h. wahrscheinlich die Tageslänge. Bei Zugvögeln ist dasselbe gefunden worden.

19. Die Häufigkeit der Kalmare schwankt jedes Jahr. Von 5 vergleichbaren Beobachtungsjahren haben die wärmeren die grösseren Fänge. Wahrscheinlich beansprucht *L. vulgaris* als Wanderer von südlicher Herkunft hohe Temperaturen, wodurch die Art veranlasst wird, in kalten Jahren nicht so weit nördlich durchzudringen als in warmen.

20. *L. vulgaris* ist in starkem Masse an das Küstenmeer gebunden. Bei Den Helder wird sie selten in mehr als 20 Meilen Entfernung von der Küste erbeutet. Das Vorkommen innerhalb der Küstenzone wird einer näheren Analyse unterworfen.

21. Im Juni findet sich die Hauptmacht der Kalmare mehr in Küstennähe als im April und Mai bzw. Juli und August. Einige Winterfänge stammen durchschnittlich aus tieferem Wasser als die Sommerfänge. Wahrscheinlich werden diese jahreszeitlichen Wanderungen durch die unter 23 zu nennende Vorliebe für höhere Temperaturen verursacht.

22. Das Wattenmeer (Gebiet 7 der Abb. 14) wird von den Kalmaren nur besucht, wenn der Salzgehalt in seinem westlichen Eingang über ungefähr 30.3 °/₀₀ steigt (Abb. 16), während die Temperatur hierbei keinen Einfluss zu haben scheint.

23. Die weiter vom Strande entfernten Teile des Küstenmeeres (Gebiete 1, 3 und 5 auf Abb. 14) werden am meisten besucht, wenn der Salzgehalt niedrig (beim Haaksfeuerschiff unter 34 °/₀₀) und das Temperaturgefälle zwischen dem Haaksfeuerschiff und der Westgrenze von Gebiet 7 gering ist. Die Tiere scheinen eine Abneigung gegen unvermischtes, salziges Nordseewasser sowie eine Vorliebe für die wärmeren Gebietsteile zu haben. Beide Eigenschaften binden sie an das Küstenmeer, wo der Salzgehalt niedriger und (im Frühling und Sommer) die Temperatur höher ist als weiter von der Küste entfernt.

24. Die Wassertiefe spielt bei der Bindung an das Küstenmeer höchstens eine untergeordnete Rolle.

25. Die ♂♂ sind in den Gebieten, die am meisten unter Landeinfluss stehen, verhältnismässig häufiger als in den anderen Gebieten (Tabelle 8, S. 261). Sie beanspruchen wahrscheinlich einen geringeren Salzgehalt oder eine höhere Temperatur als die ♀♀.

26. Die Lage der bevorzugten Laichgebiete wird beschrieben, gibt aber keinen Anlass zu weiteren Folgerungen.

27. Das Verbreitungsgebiet von *L. vulgaris* erstreckt sich über die Küsten des Mittelmeeres und der Ostatlantik zwischen 21° und 59° N.

28. Im Mittelmeer verschwindet *L. vulgaris* nicht im Winter, was zu Vergleichungen und Diskussion Anlass gibt. Für die portugiesische Küste gilt Ähnliches; hier ist die Art im Winter aber erheblich häufiger als im Sommer, was wohl auf Einwanderung beruht.

29. Entlang der holländischen Küste zieht *L. vulgaris* im Frühling vom Süden nach Norden. Die Geschwindigkeit des Zuges ist grösser als die der Resultante der Wasserbewegung; der Ortswechsel geschieht also aktiv.

30. Nach aller Wahrscheinlichkeit erreicht *L. vulgaris* die Nordsee durch die Doverstrasse, von der sie längs der belgischen, holländischen, nordwestdeutschen und dänischen Küste bis zum Kattegat und Skagerrak wandert; hier erscheint die Art erst im Spätsommer.

31. Wie die Nordseetiere im Herbste abwandern, ist ungewiss, wie auch die Lage ihrer Winterquartiere ungeklärt ist.

32. In den portugiesischen Gewässern überwintern Tiere, die wahrscheinlich den Sommer in nördlichern Gegenden verbringen.

33. Das Vorkommen an der englischen Ostküste ist ungeklärt.

34. Die Unterschiede zwischen GRIMPES Rassen *L. vulgaris breviceps* und *L. v. typica* werden vom Wachstum bedingt und sind nicht wesentlich.

35. Nach Angaben von MOORE (1937) scheint *L. vulgaris* im Irischen Meere (wie im Mittelmeer und an der südwesteuropäischen Küste, siehe oben), während des Winters nicht abzuziehen, was Anlass zu Vergleichungen mit dem Vogelzug gibt.

36. Die Wanderungen von *L. vulgaris* werden kurz verglichen mit denjenigen anderer Cephalopoden bzw. anderer Tierarten.

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COMPTES RENDUS DE LA SOCIÉTÉ NÉERLANDAISE DE ZOOLOGIE

AOÛT 1942 – JUILLET 1943

Séance du 19 septembre 1942 à Amsterdam

1. H. J. VONK (Utrecht). „Galle", „Leber" und Fettresorption bei Invertebraten.

Die anfängliche Meinung dass auch bei Invertebraten Galle und Gallensäuren vorkommen sollten, beruhte auf fehlerhaften Versuchen. Die den Gallensäuren zugeschriebenen Reaktionen wurden vorgetäuscht durch Eiweiss. In weitaus den meisten Fällen wurde bloss die „Leber" mit der Pettenkofer-Reaktion geprüft. Seit ich 1935 fand [1]), dass das Verdauungssekret von *Potamobius* imstande ist ebenso wie Galle Fettsäuren zu lösen (wahrscheinlich kolloidal), schien es mir doch nicht unmöglich, dass diese Erscheinung durch das Vorhandensein einer Gallensäure verursacht werde. Als solche kämen dann wohl Taurocholsäure oder Taurodesoxycholsäure in Betracht, da nur diese beim p_H des Krebssaftes (5) löslich sind. An völlige Isolierung ist bei der kleinen Menge Saft (50 cm³ von 100 Krebsen) gar nicht zu denken. Die Bestandteile wurden nach einem Verfahren von DOUGLAS SAUERMANN von einander getrennt. Mit der Fraktion welche abgespaltete Cholsäure enthalten könnte, wurden die Reaktionen von Pettenkofer, Jolles und Minibeck angestellt, welche alle positiv ausfielen. Der Rückstand eines verdampften Alkoholextraktes aus dem Darminhalt wurde in Puffer von p_H 3.5 gelöst. Auf Zusatz von Peptonlösung entstand ein Niederschlag. Diese Reaktion weist bei Abwesenheit anderer Eiweissfällungsmitteln und im Zusammenhang mit den Reaktionen der abgespaltenen Cholsäure, auf Taurocholsäure hin. Daneben könnte Taurodesoxycholsäure vorhanden sein, welche aber nicht durch einfache Reaktionen nachgewiesen werden kann.

2. CHR. P. RAVEN (Utrecht). The influence of lithium upon the development of *Limnaea stagnalis* L.
   Voir: Proc. Nederl. Akad. v. Wetensch., Amsterdam 45, p. 856–860, 1942.

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[1]) Zs. vergl. Pysiol. **21**, 717 (1935).

3. C. J. H. van den Broek (Utrecht). P_H-distribution and digestion in the rat's stomach [1]).

Using MacInnes & Dole's glass electrode [2]) we combine high exactitude of p_H measurement (within 0,05 of p_H unity) and a sharp localisation of the spot measured. Examining a great many points on a couple of standardised lines along the surface of the highly consistent food mass from a rat's stomach after it is laid bare, a far more detailed impression of the distribution of p_H in any moment of digestion is acquired, than by any previous method. Exact p_H measurements at 50–60 clearly discernable points in a stomach not exceeding 4 cm in length can easily be accomplished.

The influence of 3 kinds of food (bread, meat, carrots) was examined in relation to time and to percentage of food left in the stomach (calculated by dry weight in comparison to dry weight of food originally eaten). Immediately after the food is taken up the HCl, secreted in the fundus glands lowers the p_H, slowly when the food contains much albumen (bread, meat), by which the acid is partly neutralised, much faster when albumen is absent or concealed (carrots). In the 1st case it takes 6 hours before the p_H optimum of pepsine (p_H 2,2) is arrived at, in the 2nd case only 1 hour. The food, stored in the expansive cardia remains at p_H $4\frac{1}{2}$–6 for a long time, only after most of the food has disappeared the acid reaches these parts and the p_H sinks to $2\frac{1}{2}$–3. High p_H is regained, progressing from the pylorical part upwards, when the stomach becomes empty.

It is very remarkable that the rate, at which the stomach is emptied depends in exactly the same way from the kind of food eaten as does the changing of the p_H distribution. The result is that each emptying stage of the stomach is closely related to a certain typical p_H distribution, and that the kind of food was of no influence whatsoever on this relation, being able only to change the rate at which the stages succeed each other.

Some points of the rat's digestion as an omnivorous type were discussed in comparison to the herbivorous and the carnivorous type[3]).

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[1]) See also: De verdeeling van den zuurgraad in den rattenmaag, gemeten met de glaselectrode. Chemisch Weekblad **40**, 1943, p. 146.

[2]) Journ. amer. chem. soc. **52**, 1930, p. 29.

[3]) Vonk, Z. vergl. Phys. **9**, 1929; Ergebn. Enzymf. **8**, 1939, p. 55.

4. L. D. BRONGERSMA (Leyde). Sur le *Rhacophorus reinwardti* et *Rhacophorus moschata* de KUHL et VAN HASSELT.
Voir: Archives Néerlandaises de Zoologie VI, p. 341.

Séance du 17 octobre 1942 à Leyde

1. Mlle A. M. BUITENDIJK (Leyde). Are *Xantho crassimanus* A. M. Edw. and *Xantho quinquedentatus* Krauss synonyms?

The ♀♀ and young of both species are not easily separated. In the ♂♂ the first pleopod provides us with a good characteristic as the row of blunt spines on the convex side near the apex of this pleopod of *X. quinquedentatus* is missing in *X. crassimanus*. In the larger specimens of *X. crassimanus* the front is always narrow (about a third of the greatest carapace breadth), but in smaller specimens it becomes relatively broader (about half that breadth), reaching here the same breadth as in *X. quinquedentatus*. In these smaller specimens the sixth antero-lateral tooth is always situated just ventrally of the first, the latter appearing thereby double, while in *X. crassimanus* it always lies between orbit and first antero-lateral tooth. Moreover the palm and wrist of *X. crassimanus* may become granular, but they never show the granular nodules, which form a characteristic of *X. quinquedentatus*. The available evidence, therefore, points to the fact that the two groups of crabs represent distinct species.

2. J. DE WILDE (Amsterdam). Sur quelques propriétés physiques de la filure de l'Épeire diadème.
Sera publiée dans la 3ième Livraison du XXVIième Tome des Archives Néerlandaises de Pysiologie, etc., 1943.

3. D. A. HOOIJER (Leyde). On Recent and Fossil Hippopotami.

Hippopotamus amphibius L. and *H. liberiensis* Morton are the only recent representatives of their family, which in pleistocene times was spread over Africa, Madagascar, islands in the Mediterranean, Europe from Spain and Italy to England and W. Germany; India, Burma, Ceylon and Java. About thirty fossil forms have been described; a number of them is but very imperfectly known.

They first appear in the Pontian of Sicily and the Dhok Pathan zone of the Siwaliks. The Asiatic species, of which *Hippopotamus sivalensis* Falc. et Cautl., *H. sivajavanicus* (Dubois), H. *koenigswaldi* Hooijer, *H. namadicus* Falc. et Cautl. and *H. palaeindicus* Falc. et

Cautl. may be mentioned here, possess three incisors on either side of the jaw, of which the lower I2 gradually reduces. This goes hand in hand with an elevation of the orbits and a shortening of the cranial part of the skull. In all Asiatic species the lacrymal is separated from the nasal by an anterior prolongation of the frontal as in *H. liberiensis*, whereas in *H. amphibius* the lacrymal joins the nasal and excludes the frontal from contact with the maxillary.

Judging by anomalies in the dentition of *H. lemerlei* Grandidier from Madagascar and of the recent species, in the African fossil forms the lower I_3 may have disappeared. As regards the lacrymal, the skulls of *H. minor* Desmarest from the pleistocene of Cyprus and of *H. lemerlei* Grandidier sometimes exhibit an intermediate position between *amphibius* and the Asiatic forms. In the more specialized African fossil forms the orbit occupies a less central position and becomes more elevated. In this respect *H. gorgops* Dietrich from the middle pleistocene of E. Africa seems to be even more specialized than *H. amphibius*.

The relationship between the fossil forms hitherto described is not always clear; the ancestors from deposits older than Pontian are not known.

Séance du 21 novembre 1942 à Utrecht

1. L. H. Bretschneider (Utrecht). Recherches sur le mécanisme de l'oviposition chez *Limnaea stagnalis*.
   Va paraître comme publication dans ce journal.

2. P. Wagenaar Hummelinck (Utrecht). Remarques zoogéographiques sur les îles sous le vent néerlandaises (Antilles).
   Voir: Vakblad voor Biologen 24, 1943, p. 31–35, et: West-Indische Gids 25, 1943, p. 168–180.

3. P. D. Nieuwkoop (Utrecht). The determination of the lateral plate in Amphibians.

In the normal development the lateral plate is divided by the coelom into an outer and an inner layer, which respectively differentiate into somatopleure and splanchnopleure.

In the first experiment, the whole entoderm of a young neurula of *Triton taeniatus* was extirpated by cutting the ectoderm and the underlying mesoderm in the ventral median line and separating the ecto-mesodermal envelope from the entoderm. Then the mesoderm-free parts of the ectoderm were folded back against the inner side of the mesoderm. In these operated embryos, where both sides of the lateral plate have been covered by ectoderm, the inner layer of the lateral plate also contains a somatopleure-muscle-layer and forelimb, which are innervated by accessory ramifications of the spinal nerves. The presence of chromatophores also indicates that the inner layer has developed into a somatopleure.

In a second experiment, in which at the early neurula stage the lateral plates were grafted with reversal of the medio-lateral axis, the somatopleure and splanchnopleure developed normally. At this stage the lateral plates have not yet been polarized along their medio-lateral axis.

In a third experiment, after the extirpation of the entoderm, the ecto-mesodermal envelope was spread out on a collodion membrane. The neurulae grew out to large flat embryos. The outer layer of the lateral plate has developed into a normal somatopleure, whereas the inner layer, which has been adhered to the collodion, has formed a very thin indifferent epithelium.

These experiments suggest that in the normal development the ectoderm determines the outer layer of the lateral plate to somatopleure and the entoderm the inner layer to splanchnopleure; without any induction from the ectoderm or the entoderm each of them can only form an indifferent epithelium.

Séance du 23 janvier 1943 à Amsterdam

MARGARETHA BRONGERSMA-SANDERS (Leyde). The annual fish mortality near Walvis Bay (South West Africa), and its significance for paleontology.

At different occasions the paleontological significance of mass mortality has been emphasized (e.g., CUVIER's "theory" of catastrophes, early hypotheses on the origin of petroleum), afterwards to be refuted with even more stress. Recently various paleontologists (WEIGELT and others) again emphasize the importance of mass mortality. Starting from various peculiarities of the fossils they arrive at the conclusion that a great part of the vertebrates, which became fossilized, did not die in a normal way, but perished by accidents or by catastrophic events.

On November 24th, 1938 I paid a short visit to Walvis Bay. A mass mortality had taken place some days before, and fishes were scattered all over the beach. A study of the peculiarities of this region, in which a mass mortality occurs every year in the southern summer (sometimes even 4 or 5 times a year), made the real significance of such an event clear to me. When a mass mortality takes place periodically, and the intervening period is sufficiently short, it may have an important influence on its surroundings by disturbing the biological equilibrium. As a result in the Walvis Bay area (the bay itself, as well as a part of the open sea outside of it) the bottom sediment shows various peculiarities: H_2S, nearly complete absence of living organisms (anaerobic bacteria excepted), absence or excessive scarcity of remains of benthonic invertebrates, abundance of remains of fish. If the biological equilibrium is disturbed in this way, the decay of the organic remains does not proceed in a normal way, and the fish have (under certain circumstances) a good chance to fossilize. Therefore, in my opinion, a periodical mass mortality may be of importance to paleontology as well as to oil-geology.

The remarkable similarity between the phenomena in the Walvis Bay region and certain shales containing numerous fish remains supports this hypothesis; for it indicates that an event, similar to that taking place near Walvis Bay indeed played a part in the genesis of such deposits with fossil fish. The similarity exists especially with such fish shales which consist for a considerable part of the siliceous remains of diatoms (Californian miocene Monterey shales, Carpathian oligocene menolite shales). These shales are considered by most authors as source beds of petroleum. With regard to such shales the important points of the Walvis Bay area are: 1. a mass mortality of fish occurring year after year in the same place; the extent of the mortality in some exceptional years being extraordinarily great (cf. the Lompoc layer of the Californian miocene); 2. the character of the dead fish, a temperate to subtropical, near-shore shallow water fauna, benthonic fish not being absent, etc.; 3. the presence and the peculiarities of the azoic zone; 4. the sedimentation of a diatom ooze in a subtropical littoral part of the sea (normally a diatom ooze is found only in pelagic deposits of cold regions); 5. the rainlessness of the coast region: this results in various peculiarities, e.g., a great part consists of barren shifting dunes (the Kliwa sandstone, that interstratifies with, and overlies the menolite shales is explained by MRAZEC and TEISSEYRE as shifting dunes too).

This similarity stimulated me to search for the cause of the

Walvis Bay mortality, which until now was not convincingly elucidated. The hypotheses put forward in recent publications agree in the supposition that H_2S forms the cause of the mortality, although opinions differ as to the origin of the gas. In my opinion upwelling water is the indirect cause of the mortality; on account of this upwelling phosphates and nitrates, substances that regulate the quantity of the phytoplankton, are present in an excessive amount. In these very eutrophic surroundings waterbloom frequently occurs. In the warmer part of the year (southern summer) a waterbloom of certain dinoflagellates is a periodically returning phenomenon. The organisms are present in such a quantity as to discolor the water, so-called "red water". A poison produced by this waterbloom is the direct cause of the mortality.

Contrary to the above mentioned hypotheses I arrive at the conclusion that H_2S is not the cause of the mortality but the result. The presence of H_2S and of the azoic zone is the result not of the mass mortality of fish alone, but of the whole event that is connected with it: 1. a great mass of organic material is produced at one moment by a waterbloom causing fish mortality, and this creates anaerobic conditions; under these conditions sulphate reducing bacteria multiply and produce considerable quantities of H_2S; 2. the permanent elimination of benthonic invertebrates, the scavengers of the sea bottom; just as the fish these organisms will be massacred, but slow moving creatures as they are (in contradistinction to most species of fish) they cannot repopulate the area before a new catastrophe sets on. Normally a sediment containing organic remains is intensively ploughed through by these scavengers, which not only digest the organic matter, but while burrowing, bring oxygen bearing water together with aerobic bacteria to the deeper layers of the sediment. As these scavengers are permanently eliminated the conditions in the bottom sediment may remain anaerobic.

As the war makes it impossible to justify the hypothesis on the cause of the Walvis Bay mortality by researches in loco, I searched for another proof, which I found by putting the following question: If in the Walvis Bay area upwelling water is the cause of red water, and in its turn red water causes mass mortality of fish, does one find in other regions of upwelling water fish mortality caused by red water too? To answer this question I made a study of the literature of cases of discolored water and of cases of fish mortality; the answer proved to be in the affirmative. This is of importance, for now there prove to be certain regions, where mass mortality of fish (periodically or episodically) takes place on account of similar causes. Such regions undoubtedly have existed in the geological past too.

The phenomena of red water, mass mortality of fish, and the presence or absence of H_2S in different regions of upwelling water were discussed. In the literature on dinoflagellates the trio upwelling water – red water – fish mortality was already known from the Californian region. However, as far as I am aware, the question whether this trio occurs in other regions of upwelling water too, has never been put forward. The poisonousness of the red water was discussed in referring to various recent publications on mussel poisoning (SOMMER c.s., KOCH, etc.).

Besides causing mass mortality and the azoic zone upwelling water appears to be also the primary cause of the sedimentation of a diatom ooze in a littoral part of the subtropics, and just as well of the rainlessness of the coast region. If one finds traces of all these peculiarities combined in a fossil deposit, it is obvious that it originated in a region of upwelling water too. This in my opinion is the reason of the above mentioned similarity of the Walvis Bay region with certain fish shales.

Detailed studies on this subject will appear before long.

Séance du 20 février 1943 à Leyde

1. H. ENGEL (Amsterdam). Sur les Astéries du genre *Linckia*. Sera publiée dans les Résultats des Explorations du Siboga.

2. P. D. NIEUWKOOP (Utrecht). The determination of the genital ridges in the Urodeles.

The genital ridges are longitudinal folds of the peritoneum, situated on both sides of the dorsal mesentery.

Several experiments have shown that the genital ridges can only develop out of peritoneal cells. Where the coelom cavity disappeared, the genital ridges ended abruptly.

In an experiment, in which the whole entoderm of the young neurula had been extirpated, the coelom cavity did not show genital ridges, although the peritoneum and the other organs had been formed and were situated normally. The entoderm evidently activates the peritoneum, whereafter this can react upon a second, local stimulus.

From the following experiments it is evident that in the normal

Bingham (1924), qui se compose de deux parties: l'allongement, provoqué par la charge et le recouvrement, après le déchargement. La correspondance indique l'identité des propriétés fondamentales du modèle et de la masse musculaire. Cependant l'état viscoélastique des modèles est déterminé physiquement tandis que dans le muscle il doit être entretenu à l'aide de fonctions vitales (Jordan 1930). La correspondance des diagrammes d'allongement a conduit Jordan et Maas (1938) à admettre que la résistance à l'allongement est de nature plastique: l'étirement n'ajoute rien au tonus primitif; la réaction du muscle a été entièrement passive. Une augmentation de la résistance pendant l'étirement est attribuée à deux effets physiques, connus des modèles: la „consolidation" ¹) des micelles et „l'effet de chasse-neige" ¹) de la masse intermicellaire.

Cependant nous avons trouvé quelques phénomènes différant des propriétés du modèle et nous en avons conclu que la description donnée ci-dessus de ce qui se passe dans le muscle, était trop élémentaire (Postma 1935). Nous avons réussi à prouver récemment que le pied lui-même réagit à l'ètirement du muscle. Ses centres de réflexion primitifs renforcent activement la résistance tonique.

En premier lieu nous avons trouvé qu'il est possible de provoquer une inhibition du tonus au moyen d'excitation des nerfs pédieux (Postma 1942). Une inhibition distincte n'est obtenue que si la stimulation commence avant le chargement du muscle. Le pied, étant chargé et les muscles en voie d'allongement, on n'obtient qu'une faible diminution de la résistance tonique. Cette diminution de l'effet produit par le stimulus inhibitif est attribuée à l'augmentation du tonus produit par l'étirement. Ensuite nous avons étudié l'effet de la stimulation inhibitive au pied en repos. Il ne se produit aucune inhibition: sans étirement, il n'y a pas de tonus inhibitable. Par conséquent l'allongement du pied se poursuit aux dépens du raccourcissement du muscle, mais le tonus est renforcé plus ou moins intensivement. Le raccourcissement du muscle et la résistance à l'étirement variant pendant l'allongement en relation inverse, nous avons nommé ces évaluations du tonus visqueux: son niveau et son taux.

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¹) Cf. H. J. Jordan, Viscosity effects in the living protoplasm and in muscles. Verhand. Kon. Akad. Amsterdam, Afd. Natuurk. I, **15** No. 3, 2me Ed., 214, 1939.

Nous avons trouvé également que le recouvrement après le déchargement du muscle n'est pas une contre-réaction passive succédant à l'allongement, mais qu'il a une part active, effet durable de l'étirement précédent. Nous avons trouvé que, profitant du stimulus inhibitif, le recouvrement élastique [1]) n'est que susceptible de ralentissement; pendant l'hystérèse élastique [1]) le stimulus produit une baisse de la courbe; la stimulation interrompue, le recouvrement continue.

Séance du 13 mars 1943 à Utrecht

H. J. JORDAN (Utrecht). Quelques nouvelles théories sur le mécanisme de la contraction musculaire. Revue des ouvrages récents de J. LINDHARD, U. EBBECKE et A. SZENT-GYORGYI et de leurs collaborateurs.

Cette communication a été publiée in extenso dans ces Archives, voir T. VII, p. 122–152, 1943.

Séance du 10 avril 1943 à Amsterdam

1. L. F. DE BEAUFORT (Amsterdam). La règle de VON MARTENS. Sera publiée dans ces Archives.

2. P. D. NIEUWKOOP (Utrecht). The causality of the first developmental phases of the primordial germ cells in the Urodeles.

At the meeting of Nov. 8th 1941 I communicated about the results of some experiments to elucidate the origin of the germ cells.

The extirpation of the presumptive dorsal entoderm at the early gastrula stage caused a considerable decrease of the number of germ cells, in contrary to the removal of the presumptive ventral entoderm, forming the nutritive yolk material.

The removal of the presumptive mesoderm of the lateral plates and nephrogenous tissue, which is situated in the young neurula in the ventral and ventro-lateral blastoporal lips, gave rise to complete sterility, in spite of the regeneration of large parts of the lateral plates, mesonephros, germ ridges, etc.

Thus, both the dorsal entoderm and the ventro-lateral mesoderm play an important part in the development of the sex cells.

From the investigations of Vogt a.o. it is evident that in the

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[1]) Cf., également pour les détails: N. POSTMA, Versl. Nederl. Akad. v. Wetensch. Amsterdam, Vol. LII, p. 381, 1943.

young neurula only the cranial part of the mesoderm, namely the first eleven or twelve segments, has been invaginated.

After removal of the whole entoderm at this early neurula stage, the animals showed a strongly diminished number of sex cells, which were present only in the cranial part of the germinal region. Thus, it is evident that in the cranial part the sex cells have differentiated by an inductive interaction between the invaginated mesoderm and the dorsal entoderm, whereas the caudal mesoderm, which was still situated outside the blastopore, had not yet interacted with the dorsal entoderm.

Heteroplastic grafting experiments between *Triton alpestris* and *T. cristatus* have been made to solve the question, from which part (the dorsal entoderm or the ventro-lateral mesoderm) the induction comes and which contains the cell material of the presumptive germ cells.

The primordial sex cells of *Triton alpestris* and *T. cristatus* can be distinguished from each other by their different quantity of pigment granules. After heteroplastic transplation of the whole entoderm at the early neurula stage all the germ cells showed the species character of the cell material of the ecto-mesodermal envelope. They were present, however, only in the cranial part of the germinal region and were few in number. Only a few animals contained more sex cells, which were also situated in the caudal part of the trunk.

The heteroplastic transplantation of the ventro-lateral mesoderm (presumptive lateral plates) at the early yolk plug stage completely solved this question. A quantitative determination of the proportions of *cristatus* and *alpestris* cells in the trunk organs showed an obvious parallellism between the lateral plate and the sex cells, whereas this did not consist between the other organs (myotome, Wolffian duct, mesonephros, germ ridge and entoderm) and the sex cells.

From these experiments we may conclude that the primordial germ cells originate from the mesoderm of the presumptive lateral plates.

The lack of regeneration of the sex cells after removal of the presumptive lateral plates and their rather complete regeneration suggests their presence in a preformed state in this mesoderm. From several experiments it is evident that a foreign inductive action, for instance from the notochord, can suppress the differentiation of the sex cells from the lateral plate mesoderm.

In an experimental set, in which a supernumerary dorsal blastoporal lip has been implanted in the ventral lip of an other young gastrula, a displacement of the whole entoderm with respect to the neighbouring mesoderm occurred, if the two embryonal rudiments were situated exactly opposite each other. Then, the entoderm was pushed cephalad and the mesoderm caudad, by which the inductive action of the dorsal entoderm upon the ventro-lateral mesoderm was prevented. In this way sterile animals were obtained.

The results of my experiments are in accordance to the theory of the early segregation of the primordial germ cells; on the contrary, they lend no support to the theory of the origin of these cells from the germinal epithelium.

NOTES ON SOME PONTIAN MAMMALS FROM SICILY, FIGURED BY SEGUENZA

BY

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SEGUENZA (1902, 1907) described and figured a collection of mammalian fossils from Gravitelli, Sicily, including also some specimens from Scirpi and from S. Pier Niceto. Unhappily the fossil remains were destroyed by the Messina earthquake of 1908 (cf. STROMER, in LECHE, 1921, p. 42, footnote 3). No new collections from these localities have been described, and, therefore, the figures and descriptions published by SEGUENZA present the only information we possess concerning the species in this collection. A careful examination of the figures made it clear to me that a number of the specimens has been incorrectly identified by SEGUENZA.

SEGUENZA considers the fauna to be equivalent in age to those of Pikermi and Samos, i.e., Pontian; this is also the opinion of DEPÉRET (1908, p. 306 [1])), HAUG (1911, p. 1719), PARONA (1924, p. 557), and PILGRIM (1931). The latter author mentions the Carnivora from the Gravitelli fauna, and apparently agrees with the identifications by SEGUENZA.

A considerable portion of the collection was identified by SEGUENZA as *Hippopotamus* (*Hexaprotodon*) *sivalensis* Falconer et Cautley, the best known of the Siwalik Hippopotamidae of which numerous remains have been figured in Fauna Antiqua Sivalensis (cited below as F.A.S.) of FALCONER and CAUTLEY (1847). As mentioned already by STROMER (1914, p. 32) the Sicilian remains cannot belong to *sivalensis*. A careful study of the figures given by SEGUENZA made it evident to me that part of the supposed remains of *Hippopotamus* in reality belong to a bovid (pp. 319-320), and another part to a rhinoceros (pp. 322-324). These two forms have not yet been recorded from Gravitelli, and thus present two interesting new elements to its fauna. The true *Hippopotamus* remains turned out to belong to a species which I believe to be as yet undescribed, and for which I propose the name *Hippopotamus siculus* nov. spec. (pp. 305-319). The fact that the Pontian fauna of Gravitelli contains a *Hippopotamus* is of great interest, as no species of this genus has been found in other Pontian or earlier faunae of Europe and Africa 1). In Asia, *Hippopotamus* makes its first appearance in the Siwalik Dhok Pathan stage; accepting PILGRIM's correlations simultaneously with its invasion of Europe. Whereas in Asia the species seem to belong to a distinct line of evolution 2), the relationship between the African and European fossil forms is still obscure. Fossil remains of *amphibius*, of which the measurements often lie to the higher side of the range of variation, are described under different names from numerous localities in Europe and Africa, but date not earlier than Villafranchian. The smaller tetraprotodont *Hippopotamus hipponensis* Gaudry, described as hexaprotodont (pliocene: GAUDRY, 1876 3); pleistocene: OSBORN, 1910), tetraprotodont (pliocene: STROMER, 1905; pleistocene: POMEL, 1890, 1896), occurs in the Astian Vertebrate fauna of Wadi Natrun in Egypt (ANDREWS, 1902; STROMER, 1902, 1905, 1914) and also in the Villafranchian of Algeria (GAUDRY, 1876; POMEL, 1890, 1896, JOLEAUD, 1920). The record for the Siwaliks by OSBORN (1910, p.

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[1]) Subsequently DEPÉRET (1909, p. 140) states that the Gravitelli fauna probably must be referred to the extreme base of the Plaisancian.

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1) The fauna of Casino near Siena in Italy, which contains the hexaprotodont *Hippopotamus pantanellii* Joleaud, originally was supposed to be Pontian (PANTANELLI, 1879, 1886), more recent than Pikermi and Eppelsheim (MAJOR, 1875, p. 243), or uppermost Pontian (HAUG, 1911, p. 1719; JOLEAUD, 1920, p. 19). Other authors, however, consider this fauna to be post-Pontian (DEPÉRET, 1909, p. 140; OSBORN, 1910, p. 312; PILGRIM and HOPWOOD, 1928, p. 74); in his latest correlation table PILGRIM (1940, p. 11) refers the Casino fauna to the Plaisancian.

DEPRAT (1904, p. 105) mentions *Hippopotamus* spec., together with some typically Pontian Mammals, from Heria in Euboea. I have not found any subsequent notice about this find in hippopotamological literature. HAUG (1911, p. 1720) states that this record demands verification.

2) According to LYDEKKER (1884, p. 47) there is a gradual shortening of calvarium and lower jaw, and a reduction of the I_2. The final stage is represented in *Hippopotamus palaeindicus* Falconer et Cautley, originally supposed to be tetraprotodont (F.A.S., pl. 57 fig. 5), in which species I_2 is only small and situated on a level with the upper margin of the very large I_1 and I_3 (LYDEKKER, 1884, pl. VI fig. 2). LYDEKKER is not certain as to which of the incisors becomes reduced in the upper jaw. However, in *sivalensis*, I^3 being the smallest already (F.A.S., pl. 62 fig. 3), one might have concluded that it is the third incisor which reduces in the upper jaw, as shown by VON KOENIGSWALD (1934) on the evidence of material from Java.

3) For the exact type locality see PAPIER (1878).

313) must be a slip of the pen of this author. *Hippopotamus imaguncula* Hopwood [1]) (original reference not seen), from the pleistocene Kaiso Bone-beds, S.E. of Lake Albert in Central Africa, is stated (HOPWOOD, 1929, p. 105) to be intermediate between *lemerlei* and *liberiensis;* the limb-bones partake more of the characters of the latter, whereas the dentition has more in common with the former. *Hippopotamus pentlandi* Von Meyer, only differing from *amphibius* in its smaller size, is first mentioned under that name by VON MEYER (1832, p. 533; 1843, p. 582) from pleistocene caves in Sicily. Teeth are figured by BLAINVILLE (1847, Atlas, pls. VII-VIII Palermo specimens). It has been recorded too from pleistocene caves in Malta and Crete (ADAMS, 1866, p. 594, FALCONER, 1868 II, pp. 299-301; ADAMS, 1877, p. 187). The remains described as "*Hippopotamus pentlandi* Falconer" by SEGUENZA (1900), from Taormina in Sicily and by BORTOLOTTI (1904) from Perugia in Italy, however, must be referred to *Hippopotamus amphibius* L. Also part of the remains, figured under the name *pentlandi* by GREGORIO (1924, 1925 [2])) from caves in Sicily, belong to the recent species, which is known to occur in the fossil state in the Sicilian caves as well. *Hippopotamus melitensis* Major (1902*b*, p. 198, footnote 6), from pleistocene caves in Malta and Crete, is mentioned by FALCONER (1868 II, p. 307), and ADAMS (1877, p. 187) as "*Hippopotamus minutus*", the name given to teeth from Crete which were figured by BLAINVILLE (1847, Atlas, pls. VII-VIII). These teeth, however, possess a structure as complicated as in *amphibius* and *pentlandi*, and are intermediate in size between the latter and the pigmy hippopotamus from Cyprus. The correct name of the pleistocene Cyprus form is *Hippopotamus minor* Desmarest (1822, p. 388), which antedates *H. minutus* Cuvier (1824, p. 527). This species has originally been described and

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[1]) This species is recorded too (ARAMBOURG, 1934, p. 307) from the fossil vertebrate fauna N. of Lake Rudolph in Abyssinia. This fauna, first mentioned by HAUG (1911, p. 1727), contains both *Deinotherium* and *Hippopotamus*. The former genus is represented by a species, described as *Deinotherium bozasi* (ARAMBOURG, 1934, p. 309; not mentioned by OSBORN (1936)). According to JOLEAUD (1920, p. 22) the hippopotamus is not different from *amphibius*. HOPWOOD (1929, p. 104, 111) regards the *Deinotherium* as geologically older than the remainder of the fauna; this is, however, not confirmed by ARAMBOURG (1934, p. 306).

[2]) The plates of GREGORIO are very badly drawn; it is, however, almost certain that the bone figured as "tibia" (GREGORIO, 1924, pl. XIII fig. 1) is a radius of a bovid.

figured as "petit hippopotame fossile" by CUVIER (1804, 1821), based on teeth and bones from blocks of unknown origin. Afterwards some additional specimens are mentioned (CUVIER, 1822, pp. 382-383); the specimens also have been figured by BLAINVILLE (1847, Atlas, pl. VI). In 1901 this species was rediscovered in the pleistocene of Cyprus, viz., in an ossiferous breccia at Chrysostomo near Kythraea and in caves, e.g., that of Haghios Jannos, Cape Pyla. As even the matrix agrees with that described by CUVIER (MAJOR, 1902*a*, p. 110), it is almost certain that CUVIER's blocks originated from Cyprus [1]). The species (a reconstructed skeleton is figured by BATE, 1906, pl. XV), is as large as the recent pigmy hippopotamus from Liberia, *H. liberiensis* Morton, but differs in important features, e.g., in the lacrymal being in contact with the nasal, in the elevation of the orbit and in the dentition. Finally *Hippopotamus lemerlei* Grandidier (in EDWARDS, 1868*a*, p. 1165; 1868*b*, p. 375) must be mentioned here. This subfossil species from Madagascar is more fully described and figured by GULDBERG (1883) as *H. madagascariensis*, and by GRANDIDIER and FILHOL (1894) as *H. lemerlei* and as *H. leptorhynchus*. The skeleton is figured by FILHOL (1895, p. 89), MAJOR (1920*b*, pl. XII) and OSBORN (1910, p. 433, fig. 186). The species is intermediate in size between *hipponensis* and *liberiensis;* the dentition agrees with *amphibius*, of which the Madagascar form, however, differs in some primitive cranial features, e.g., the lesser elevation and the more central position of the orbit (MAJOR, 1896, 1902*b*). Two premaxillary bones from Ampasambazimba are described by JOLEAUD (1923, p. 117). It is interesting that the exceptional variations in the milk dentition of *amphibius*, noticed by me (HOOIJER, 1942, pp. 189, 190, 193), occur in *lemerlei* too. In the left lower jaw with milk dentition figured by JOLEAUD (1920, pl. 1) the pd_1 is double rooted; in a young upper jaw of the same species DIETRICH (1928, p. 24) observed that the pd^1 has not developed. Various opinions have been expressed as to the relationship between the African and European fossil Hippopotamidae and their recent African representatives, I shall return to this problem later on.

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[1]) The ossiferous breccia of Kythraea in Cyprus was already known at the end of the 17th century to a Dutch traveller DE BRUYN (LE BRUN), who figured a bone from it, which he stated to resemble a human radius. From the figure MAJOR (1902*a*, p. 110) supposed the bone to be a femur of *Hippopotamus*. In my opinion (MAJOR cites the Delft edition (1700) of LE BRUN's work, I saw the Amsterdam edition of 1714, which is cited by GAUDY (1862, p. 153)) the bone might belong to *Hippopotamus minor* Desmarest, but it is certainly a humerus and not a femur (LE BRUN, 1714, fig. 193).

Hippopotamus siculus nov. spec.

Diagnosis: Number of incisors unknown, but very probably hexaprotodont. Upper C with deep longitudinal groove posteriorly. Trefoil pattern of molars less developed than in *sivalensis*, *amphibius*, *melitensis*, and *hipponensis*, but more stressed than in *liberiensis*, *minor*, and *pantanellii*. Size of the teeth about equal to that in *sivalensis* and *pantanellii*, and smaller than in *amphibius*. Ventral spine on third cervical vertebra not so prominent as in *sivalensis*. Radius with crest between articulation surfaces for scaphoid and lunar directed more antero-posteriorly, and surface for articulation with scaphoid relatively smaller than in *sivalensis*. Articulation surface for cuneiform on unciform more concave, and that for lunar narrower in respect to the former than in *sivalensis*. Astragalus with small difference in level between facies articularis cuboidea and fac. art. navicularis; no tuberosity below the medial ridge of the trochlea; broad and shallow fossa medially of facies articularis calcanea posterior. The postcranial remains display the greatest resemblance to *amphibius*, but are decidedly smaller.

Description and comparison.

Milk dentition: The "frammento di mascella inferiore di sinistra" (fragment of left lower jaw) (SEGUENZA, 1902, pp. 162-163, pl. VII figs. 1-3) is a portion of a left maxillary with pd^3, pd^4, and M^1. The pd^3 is broken off along the alveolar border, the length of the remaining part of this tooth is 30 mm, maximum breadth 16 mm. The pd^4 is damaged; the tooth is molariform as in all species of *Hippopotamus* of which this tooth is known; the length is 34 mm, the breadth 31 mm. The "metà anteriore di un premolare" (anterior half of a premolar) (SEGUENZA, 1902, p. 163, pl. VII fig. 20) might be a left pd^4; from the only figure given of this fragment its position in the dentition is not certain. The breadth is given as 27.5 mm.

The left pd$_2$ (SEGUENZA, 1907, pp. 112-113, pl. VI figs. 19-20) has a convex labial and a flat lingual surface, as in *amphibius* and *liberiensis*; this is also the case in *sivalensis* (F.A.S., pl. 61 fig. 6), in which species this tooth is somewhat longer than in *siculus*. In

SEGUENZA's figure some very weak posterior accessory cusps are to be seen, which in *amphibius* sometimes are more distinct (see, e.g., HOOIJER, 1942, pl. X). The length is 25 mm, the breadth 11 mm.

The "terzo premolare di sinistra" (left third premolar) (SEGUENZA, 1907, p. 113, pl. VI fig. 16) is a right pd_3, and the "dente omologo di destra" (corresponding right tooth) (l.c., figs. 14-15) a left pd_3. The length is 26 mm, the breadth 10-13 mm. The main cusp has a convex labial surface, which is more smooth than the flat lingual surface. Of the two posterior cusps the labial is the larger; a small cusp is present at the anterior side of the tooth. This is also the case in *amphibius*, *hipponensis* (STROMER, 1914, pl. III fig. 7*b* = left pd_3) and in *liberiensis*; there is no reason to believe that in *sivalensis* (F.A.S., pl. 61 fig. 6) it would be otherwise. The tooth of *sivalensis* is distinctly longer than that of *siculus*. In *minor* (MAJOR, 1902*a*, pl. IX fig. 1 d2) this tooth is more simply built; the two posterior cusps are relatively smaller, and the anterior is missing.

The milk premolars of the fossil species of *Hippopotamus* do not afford very distinct specific characters apart from differences in size.

Incisors: In 1902, when he had no incisors at his disposal, SEGUENZA referred his material to a hexaprotodont species. In his second paper on the Gravitelli fauna (SEGUENZA, 1907, p. 119) he mentioned three pairs of incisors; four of these teeth are figured, their measurements in mm are given below:

	SEGUENZA, 1907, pl. VII	SEGUENZA, 1907, p. 119	present paper	length	greater diameter	smaller diameter
A	fig. 13	I_1	I_1	(165)	23	20
B	fig. 14	I_3	?I^1	(145)	25	19
C	fig. 15	I_3	?	(84)	—	—
D	fig. 16	I_2	?I^2	(130)	24	20

The length of the incisors is given in parantheses, as it appears from the figures (their scale is not mentioned, but must be $\frac{1}{2}$ nat. size) that, apart from the worn tips, the teeth are not complete.

A is the longest and almost straight, and according to the text slightly elliptical in cross section.

B is curved, compressed, and twisted for about 90°. The abrasion surface is situated at the inner curve (fig. cit., lower side at the left). According to the text, both B and C possess a groove on both sides; the figures indeed show a distinct longitudinal groove on the broad surfaces of both teeth.

D is curved also; the abrasion surface, long and distinct, is situated at the outer curve, and shows longitudinal scratches.

Taking into consideration the variability of the incisors in the recent species, it is not always possible to indicate with certainty which position a separate incisor must have occupied in the dentition. A, however, is only comparable to, and may safely be regarded as, an I_1. As to B and C: a distinct longitudinal groove on the two broad surfaces is found in the I^1 of *amphibius* and *liberiensis*, and in the I_2 of *amphibius*. I found an I_2 of *amphibius* (Leiden Museum, cat. ost. n), which is also twisted about 90°. On lower incisors in hippopotami the abrasion surface stands about vertically. Supposing that B is a lower incisor, and, therefore, orientating it so that its abrasion surface is vertical, the proximal part of the tooth proves to be dorsoventrally compressed. In all twisted teeth I studied previously, the proximal part has the shape of normal teeth. Assuming this also to be the case in B, and thus further assuming the normal (not twisted) incisor in the same position in the dentition to be dorsoventrally compressed too, the equivalent of B is found in the I_2 occasionally occurring in *liberiensis* (Leiden Museum, cat. ost. a and c), or in the I_3, which occurs as a great exception in *amphibius* (Leiden Museum, cat. ost. d, HOOIJER, 1942, p. 193, fig. 2). However, B is curved in the same way as normal upper incisors. Twisted upper incisors occur too. In respect to the length of the tooth, B can more safely be regarded as probably being an I^1. The small fragment C cannot be identified with any degree of certainty. Scratches, similar to those present on the abrasion surface of D, may be found on upper incisors. In shape and position of the abrasion surface, D resembles one of the variations of the I^2.

Thus, none of the incisors presents particularities which point with certainty to its being an I_3, but nevertheless there is strong evidence that *siculus* is hexaprotodont: in relation to the size of M_2, the I_1 of *siculus* is as small as in *pantanellii* (PANTANELLI, 1879, pl. IV fig. 5), the only ascertained hexaprotodont species of *Hippopotamus* in Europe and Africa.

Canini: The upper C of *siculus* (fig. 1 *a-b*) possesses a broad and deep longitudinal groove in the concave posterior surface; in this

	siculus	*sivalensis*	*pantanellii*	*hipponensis*	*lemerlei*		*liberiensis*		*amphibius*	
I^1 gr. diameter	?25	ca. 22	?25	?15	15	10	11	9	27	40
sm. diameter	?19	ca. 11	?20	?10.5	12	8.5	7	8	24	36
I^2 gr. diameter	?24	ca. 22	—	18	11	9	10	9	24	31
sm. diameter	?20	ca. 14	—	13.5	10	7.5	8	8	20	27
I^3 gr. diameter	—	ca. 15	—	—	—	—	—	—	—	—
sm. diameter	—	ca. 10	—	—	—	—	—	—	—	—

	siculus	*sivalensis*		*pantanellii*		*hipponensis*			*lemerlei*			*liberiensis*		*amphibius*	
I_1 gr. diam.	23	ca. 24	34	22	21	?23	25	20	13	21	22	15	14	31	59
sm. diam.	20	ca. 22	—	22	18	—	20	16.5	—	—	—	14	12	—	—
I_2 gr. diam.	—	ca. 21	25	21	—	?20	18	16	11	15	19	9	7	21	39
sm. diam.	—	ca. 19	—	18	—	—	18	12	—	—	—	8	7	—	—
I_3 gr. diam.	—	ca. 21	33	18	—	—	—	—	—	—	—	8	—	—	—
sm. diam.	—	ca. 18	—	16	—	—	—	—	—	—	—	7	—	—	—

feature the Sicilian form resembles *sivalensis* (fig. 1 *c-d*); this has not escaped SEGUENZA's notice. There are, however, differences. The transverse diameter is relatively smaller in *siculus* as compared with *sivalensis*. In *siculus*, both on the lateral and the medial surface (the latter is not covered with enamel) there occurs a shallow but distinct groove; that on the lateral surface does not occur in *sivalensis*. The species agree in the presence of fine longitudinal grooves on the medial surface (*siculus:* SEGUENZA, 1902, pl. VII fig. 13; 1907, pl. VI fig. 11; *sivalensis:* F.A.S., pl. 62 figs. 8 and 9).

The deep posterior groove in the upper C is a feature of Asiatic hippopotami, and is found also in *liberiensis* (fig. 1 *e*). Moreover, in the latter species a shallow but distinct groove occurs on both the lateral and the medial surface. In the other species of *Hippopotamus* the posterior groove in the upper C is much shallower. In *hipponensis* (fig. 1 *f*) it is situated almost in the middle of the tooth, the medial and the lateral grooves are lacking. In *amphibius* (fig. 1 *g*) there are weak grooves on the sides, that on the medial surface may be absent, the posterior groove is situated to the medial side of the axis of the tooth. Measurements or cross sections of the upper C of *minor* are not given in literature, but when we compare the anterior view of the upper C (fig. 2 *a*) with that of *liberiensis* (fig. 2 *b*), it is evident that in *minor* the posterior groove is not only shallow, but also closer to the medial side than in *liberiensis*.

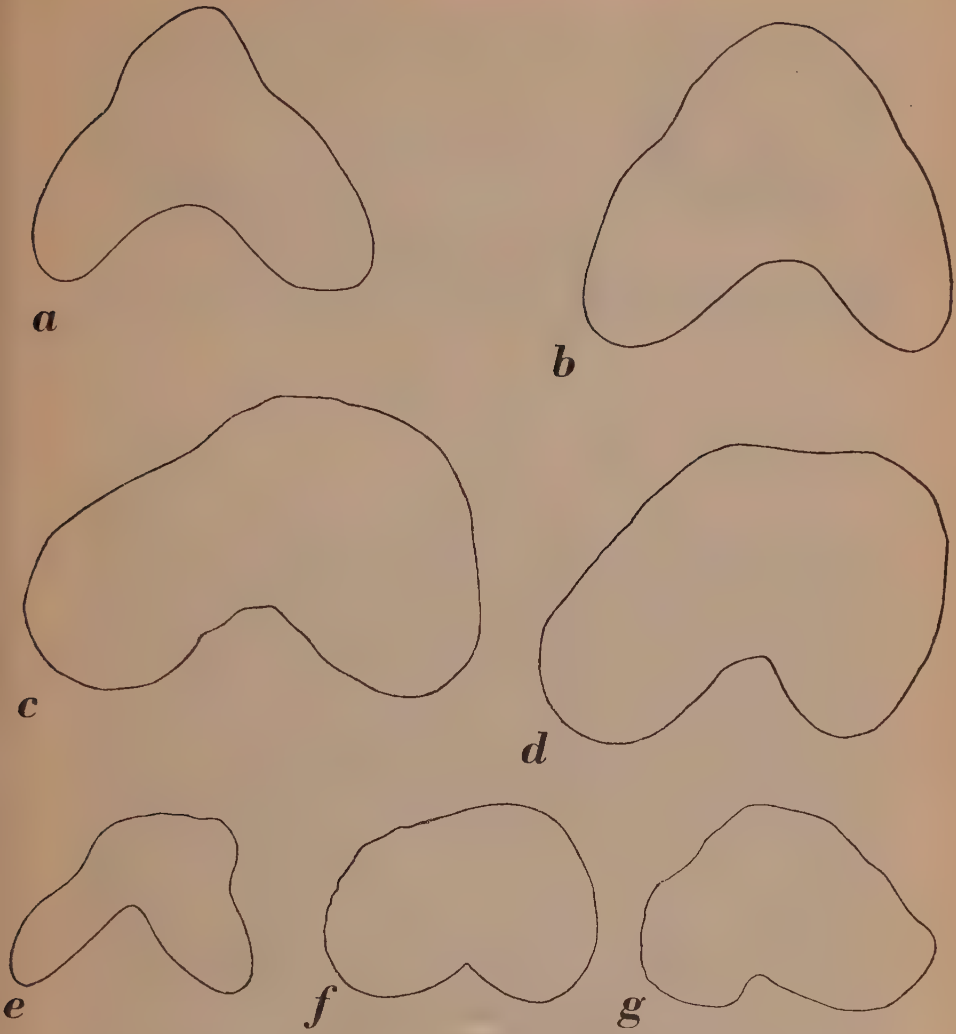

Fig. 1. Outlines of upper C in cross section. With the exception of fig. *b* all specimens are of the left side; the posterior surface is below, the medial at the left, and the lateral at the right in the figures.

a-b Hippopotamus siculus nov. spec. (after Seguenza, 1902, pl. VII figs. 12 and 14); *c-d H. sivalensis* Falconer et Cautley (after F.A.S., pl. 62 figs. 8*a* and 9*a*); *e H. liberiensis* Morton (Leiden Museum, cat. a); *f H. hipponensis* Gaudry (after Stromer, 1914, pl. 1 fig. 2*b*); *g H. amphibius* L. (Leiden Museum, cat. c). All figures natural size.

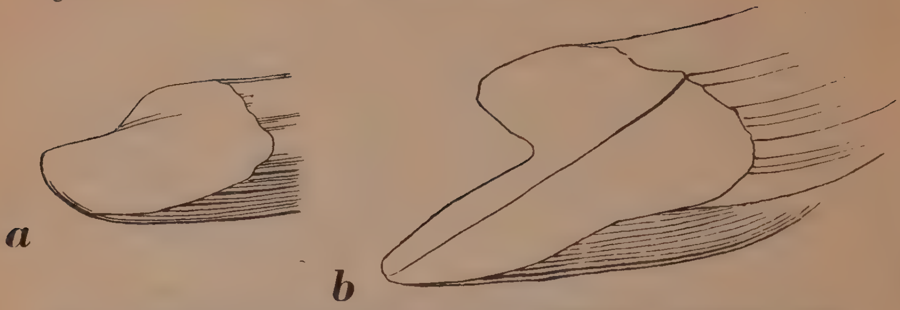

Fig. 2. Anterior view of upper left C. *a H. minor* Desmarest (after Bate, 1906. p. 244 fig. 1); *b H. liberiensis* Morton (Leiden Museum, cat. *a*). Natural size.

	siculus 1)	*sivalensis*	*hipponensis*	*liberiensis*	*amphibius*
Upper C ant. post.	37 43 —	40 39	25	25 19	30 40
transv.	44 48 56	60 55	34	34 29	38 47

The lower right C of *siculus* (Seguenza, 1907, pl. VII figs. 11-12) is feebly grooved longitudinally. The medial surface of the tooth is not figured by Seguenza; he identified the tooth incorrectly as a left canine, and, therefore, indicates the lateral surface as "lato int." (inner surface) in the explanation of the figure (l.c., p. 122). Therefore, in speaking of a shallow but distinct longitudinal groove in the middle of the "lato esterno" (outer side), Seguenza (l.c., p. 118) meant the typical groove on the median surface, also found in *amphibius*, which is absent or only very shallow in Asiatic hippopotami (F.A.S., pl. 57 fig. 8*a*, pl. 62 fig. 4*a*). This groove in *hipponensis*, in comparison with *amphibius*, is "sehr flach" (very shallow) (Stromer, 1914, p. 6); this is also the case in *minor* (Blainville, 1847, Atlas, pl. VI upper side, middle figure; Major, 1902*a*, pl. IX fig. 7), whereas in *liberiensis* the groove is completely absent, the medial surface of the lower C being convex instead of flat. In *pantanellii* (Pantanelli, 1879, pl. IV fig. 1) the medial groove does occur; the enamel seems to be transversally striated, whereas it is longitudinally grooved in *amphibius*.

	siculus	*sivalensis*	*hipponensis*	*lemerlei*	*liberiensis*	*amphibius*
Lower C longer d.	62	61	44 55 30.5	20 37	27 31	39 77
transv.	32	—	— — 17	— —	14 21	25 49

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[1] The measurements given by Seguenza are not convenient; those given in the table are taken from the figures.

Premolars: The "secondo premolare di un individuo molto adulto" (second premolar of a well adult individual) (SEGUENZA, 1907, p. 114, pl.VI figs. 17-18) is a left P^2, the tooth is comparatively little worn. The P^2 of *sivalensis* (F.A.S., pl. 62 figs. 1 and 3) is shorter and broader; in both species, as in *amphibius* and *liberiensis*, the cingulum is widened at the posterolingual side.

The "4° premolare inferiore di destra" (lower right fourth premolar) (SEGUENZA, 1907, p. 118, pl. VII figs. 9-10) is a P^4, very probably a left. This tooth in hippopotami is subject to rather wide individual variations; therefore, comparisons are useless.

	siculus	*hipponensis*		*lemerlei*			*liberiensis*	*amphibius*	
P^2 length	39	—	—	26	22	23	22	33	39
breadth	24	—	—	16	14	13	15	22	27
P^4 length	36	22	20	23	21	23	19	26	35
breadth	29	22	17	23	22	18	18	25	38

The "2° premolare di sinistra" (left second premolar) (SEGUENZA, 1907, p. 118, pl, VII figs. 5-6) is a right P_2. The main cusp is somewhat worn anteriorly. There is a feeble indication of a lingual accessory cusp, which in *hipponensis* (STROMER, 1914, pl. III fig. 1) is very distinctly developed. In *sivalensis* (F.A.S., pl. 62 fig. 2) the lingual cusp is less developed than in *hipponensis*, in both species the tooth is narrower than in *siculus*. In *amphibius* and *liberiensis* a lingual accessory cusp always is more or less developed. If the premolar of *pantanellii* (PANTANELLI, 1879, pl. IV fig. 3) is a P_2, as supposed by STROMER (1905, p. 117; 1914, p, 32), *pantanellii* is rather primitive in this respect:there is even no trace of a lingual accessory cusp.

The right P_3 of *siculus* (SEGUENZA, 1907, p. 118, pl. VII figs. 7-8) has a more distinct lingual cusp than its P_2, though still less developed than in *sivalensis* (F.A.S., pl. 62 figs. 2 and 5) and especially when compared with *hipponensis* (GAUDRY, 1876, pl. XVIII fig. 5*a*; this tooth I do not regard as a P_2, as supposed by GAUDRY, but as a P_3, in agreement with STROMER (1914, p. 8)). In *amphibius* and *liberiensis* P_3 is always larger than P_2 and has a more developed lingual accessory cusp.

	siculus	*pantanellii*	*hipponensis*		*lemerlei*		*liberiensis*	*amphibius*	
P_2 length	—	?32	29	—	24	22	17	29	41
breadth	27	—	19	—	14	13	12	18	24
P_3 length	—	—	35	32	27	23	21	37	44
breadth	26	—	—	19	15	15	12	22	27

Molars: The left M^1 is present in the maxillary (Seguenza, 1902, pp. 162-163, pl. VII figs. 1-3); a right M^1 is figured too (Seguenza, 1907, pl. VI figs. 9-10). The left seems to be little worn, but is severely damaged, the metaconule 1) only is entire. The crenulated cingulum, surrounding the whole crown, is similar to that in *hipponensis* (Andrews, 1902, pl. XXI fig. 5; this is a left M^1 and not an M^2; in this respect I agree with Stromer (1905, p. 111)). In *amphibius* the cingulum especially is developed anteriorly and posteriorly. The right M^1 is better comparable to *sivalensis*; the trefoil pattern being visible, at least in part. A right M^1 of *sivalensis*, figured in F.A.S. (pl. 62 fig. 1) is more worn than that of *siculus*, but nevertheless the vertical grooves on the anterior and posterior sides of the cusps are sharper and deeper than in *siculus*. This difference is still more striking, when we compare the molar of *siculus* with an M^1 of *amphibius* in the same degree of wear. An M^1 of *amphibius* in the same degree of wear as the molar of *sivalensis*, however, agrees with the latter in the pronounced trefoil pattern. The molars of *sivalensis* in general are not inferior to those of *amphibius* as regards the structural complexity. When comparing the M^1 of *siculus* with that of *hipponensis*, the grooves in the cusps seem to be sharper than in *siculus*; the similarity as regards the cingulum is mentioned already above. In *liberiensis*, however, the trefoil pattern is less developed than in *siculus*, and still less in *minor* (Major, 1902*a*, pl. X fig. 6).

The left M^2 of *siculus* (Seguenza, 1902, p. 163, pl. VII figs. 10-11) is fragmentary, only the paracone and metacone are present. Fortunately the corresponding molars in *sivalensis* (F.A.S., pl. 62 fig. 1) and in *hipponensis* (Stromer, 1914, pl. 1 fig. 5) are in the same stage of wear. In the molars of the latter two species, as in *amphibius* and *pentlandi* and *melitensis* (Blainville, 1847, Atlas, pl. VII) the grooves in paracone and metacone are deeper and sharper than in *siculus*. This is especially clear, when comparing

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1) The following nomenclature is used in the present paper:

Upper molars:	protocone	antero-internal cusp
	paracone	antero-external cusp
	metaconule	postero-internal cusp
	metacone	postero-external cusp
Lower molars:	metaconid	antero-internal cusp
	protoconid	antero-external cusp
	entoconid	postero-internal cusp
	hypoconid	postero-external cusp
	hypoconulid	"talon" of M_3

the length of the anterior lobe of the metacone in *siculus*, *sivalensis*, and *hipponensis*, which has not yet become confluent with paracone or metaconule. In all species mentioned and also in *minor* (BLAINVILLE, 1847, Atlas, pl. VI at the left side of the astragalus) the paracone is more simply built than the metacone. In the molar of *siculus* the labial cingulum is higher along the paracone than along the metacone; this is also the case in *amphibius*, *hipponensis* (STROMER, 1905, pl. XX fig. 2), *liberiensis* and *minor*.

The "secondo molare superiore di sinistra" (upper left second molar) (SEGUENZA, 1907, pp. 108-109, pl. VI figs. 7-8) is a right M^3. The tooth is almost unworn, a part of the cingulum at the base of the protocone is missing; the posterior cusps, therefore, in the complete tooth will not have been higher than the anterior, probably they even were somewhat lower. When seen from below, the posterior cusps are narrower than the anterior; this is a common feature in hippopotami, least distinct in *minor* (MAJOR, 1902*a*, pl. X fig. 6). When comparing the molar of *siculus* with the slightly worn right M^3 of *sivalensis* (F.A.S., pl. 62 fig. 1) and with the unworn left M^3 of *hipponensis* (ANDREWS, 1902, pl. XXI fig. 4) the grooves in the cusps of the molar of *siculus* are less distinct. In an unworn M^3 of *liberiensis*, however, the grooves are less distinct than in *siculus*, but still more than in *minor* (MAJOR, l.c.).

	siculus		*sivalensis*		*hipponensis*	*lemerlei*		*minor*	*liberiensis*	*amphibius*	
M^1 length	40	41	34	46	36	29	24	20	23	37	54
breadth	37	45	44	38	35	28	22	20	22	36	45
M^2 length	45	—	42	53	41	34	36	24	30	45	62
breadth	—	—	53	44	39	36	28	24	27	41	51
M^3 length	44	—	48	53	39	39	38	27	27	47	62
breadth	44	—	50	—	39	38	29	27	27	45	53

SEGUENZA (1907, p. 117, pl. VII figs. 3-4) figures a strongly used right M_1, and a fragment of a right mandibular ramus with an unworn M_1 and an erupting M_2 (l.c., pp. 109-110, pl. VI figs. 1-3). The strongly used M_1 is worthless for comparison. The unworn M_1 of *siculus* has the longitudinal valley between metaconid and protoconid situated labially of that between entoconid and hypoconid, whereas in *sivalensis* (F.A.S., pl. 61 fig. 6) both valleys are found in the same straight line. In both species the posterior cingulum is highest at the entoconid. The features differentiating the molar of *siculus* from that of *amphibius* are: the deeper longitudinal valley, the slenderness of the unworn cusps (especially metaconid and entoconid), and the less stressed trefoil pattern. These are the characters of a *liberiensis* molar, in which, however, the lobes obstructing the transverse valley are less developed. In the M_1 of *minor* (MAJOR, 1902*a*, pl. X fig. 4) the grooves in the cusps are almost invisible.

The right M_2 and M_3 (SEGUENZA, 1907, pp. 116-117, pl. VII figs. 1-2) are figured from the labial and the lingual side only. It is, however, clearly visible that there is no posterior lobe on the entoconid. In all species of *Hippopotamus*, of which the tooth is known, *pantanellii* excepted, the entoconid of the M_2 is more simply built than the hypoconid. In species with distinct trefoil pattern (*sivalensis*, *amphibius*, *pentlandi*, *melitensis*) the feature is more striking than in species in which the trefoil pattern is less stressed (*hipponensis*, *liberiensis*, *minor*). In *pantanellii*, however, (PANTANELLI, 1879, pl. IV fig. 4; this tooth is not a "molare sup." as supposed by PANTANELLI (l.c., p. 327), but a left M_2; I agree with STEHLIN (1900, p. 434-435) in this respect) the entoconid is as large as, and even seems larger than, the hypoconid. When comparing this molar with the corresponding tooth of *minor* (MAJOR, 1902*a*, pl. X fig. 4), it appears that in the latter species a feeble posterior groove is present in the hypoconid, this groove does not occur in *pantanellii*. Thus not *minor*, but *pantanellii* shows "the most generalized condition of all the known forms" (MAJOR, 1902*a*, p. 111). From a comparison of the molar of *pantanellii* with that of *hipponensis* (STROMER, 1914, pl. III fig. 2*a*), which is also decidedly smaller, it is evident that the Casino form cannot be identical with *hipponensis*; an opinion originally expressed by PANTANELLI (1879, p. 318), in which he is followed by STEHLIN (1900, p. 435), SEGUENZA (1902, p. 166), OSBORN (1910, p. 313) and PRATO (1912, p. 28), which authors all accepted *hipponensis* as being hexaprotodont. It is also evident that the Gravitelli form does not belong to *pantanellii*; this has been stated by AIRAGHI (1921, p. 416 footnote 1).

The right M_3 of *siculus* is different from *amphibius* in the more

<table>
<tr><th></th><th colspan="2"><i>siculus</i></th><th colspan="2"><i>sivalensis</i></th><th><i>pant.</i></th><th colspan="2"><i>hipponens.</i></th><th colspan="2"><i>lemerlei</i></th><th><i>pentlandi</i></th><th><i>melit.</i></th><th><i>minor</i></th><th colspan="2"><i>liberiensis</i></th><th colspan="2"><i>amphibius</i></th></tr>
<tr><td>M_1 length</td><td>40.5</td><td>41</td><td>31</td><td>38</td><td>—</td><td>—</td><td>—</td><td>29</td><td>29</td><td>—</td><td>—</td><td>22</td><td>23</td><td>22</td><td>42</td><td>57</td></tr>
<tr><td>breadth</td><td>28</td><td>32</td><td>24</td><td>33</td><td>—</td><td>—</td><td>—</td><td>28</td><td>19</td><td>—</td><td>—</td><td>15</td><td>18</td><td>18</td><td>33</td><td>39</td></tr>
<tr><td>M_2 length</td><td>46</td><td>50</td><td>43</td><td>48</td><td>45</td><td>38</td><td>32</td><td>26</td><td>29</td><td>—</td><td>—</td><td>25</td><td>27</td><td>28</td><td>55</td><td>65</td></tr>
<tr><td>breadth</td><td>35</td><td>39</td><td>31</td><td>39</td><td>33</td><td>24.5</td><td>30</td><td>26</td><td>22</td><td>—</td><td>—</td><td>17</td><td>21</td><td>21</td><td>34</td><td>47</td></tr>
<tr><td>M_3 length</td><td>63</td><td>—</td><td>56</td><td>72</td><td>—</td><td>—</td><td>58</td><td>59</td><td>50</td><td>56—63</td><td>47</td><td>33</td><td>36</td><td>—</td><td>64</td><td>81</td></tr>
<tr><td>breadth</td><td>35</td><td>—</td><td>33</td><td>41</td><td>—</td><td>—</td><td>31</td><td>29</td><td>23</td><td>—</td><td>—</td><td>16</td><td>21</td><td>—</td><td>35</td><td>46</td></tr>
</table>

slender cusps and the larger hypoconulid; the Gravitelli molar seems to differ in the same characters from *sivalensis* (F.A.S., pl. 62 fig. 2).

Post-cranial skeleton: A third vertebra cervicalis is described and figured by SEGUENZA (1907, pp. 110-112, pl. VI figs. 4-6). The arcus vertebrae and the dorsal boundary of the foramina transversaria are missing. The ventral part of the processus transversus has almost entirely broken off, and there are injuries, e.g., at the upper side at the left of the caput vertebrae. However, a difference from *sivalensis* has not escaped SEGUENZA's notice, viz., that the ventral spine is not so prominent as in the Siwalik species 1). Both *sivalensis* (F.A.S., pl. 63 fig. 1*a*) and *liberiensis* are

vertebra cervicalis III	*siculus*	*amphibius*2)		*sivalensis*	*liberiensis*3)
Length of corpus (centr.)	40	53	—	—	—
Id. (dorsal)	46	58	75	ca. 50	—
Id. (ventral)	44	59	68	ca. 48	33
Breadth over proc. transv.	128 4)	—	284	—	110
Breadth of caput	57	76	75	ca. 68	30
Height of id.	54	58	70	ca. 53	ca. 30
Breadth of fossa	74	91	95	ca. 72	ca. 35
Height of id.	55	65	70	ca. 62	32
Gr. diam. for. transv.	14	17	18	ca. 13	6
Sm. diam. of id.	10	14	13	ca. 9	5

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1) On plate 63 of F.A.S. both fig. 12*a* and fig. 12*b* occur twice. The third cervical vertebra is figured in fig. 12 (posterior view), the lower fig. 12*a* (anterior view), and in the two figs. 12*b*, of which the upper presents a ventral view and the lower (fig. 12*b* bis) a right view. The second fig. 12*a*, immediately above the figs. 11*b* and 12, must be marked, however, as fig. 11*c*, for it presents a ventral view of the sixth cervical vertebra, which is represented in figs. 11, 11*a*, 11*b*. This vertebra cannot be the third, as is evident from the lower position of the foramina transversaria. The incorrect numbering was not noticed by LYDEKKER (1885, p. 308). SEGUENZA was led astray by it, and therefore (SEGUENZA, 1907, p. 111) states that from the "due esemplari di terza vertebra cervicale illustrati dai predetti autori (i.e., FALCONER and CAUTLEY, 1847), l'uno presenta tale cresta assai più prominente che nell' altro . . ." (two specimens of the third cervical vertebra figured by the above mentioned authors, one presents this spine much more prominent than the other); therefore he regards the difference between the Sicilian vertebra and *sivalensis* as not important. In fact, he only noticed that the ventral spine on the third cervical vertebra is much more prominent than that on the sixth.

2) The measurements are taken from the skeletons in the Leiden Museum (cat. ost. a) and the Zoological Museum at Amsterdam (no. 183) respectively.

3) From the skeleton in the Leiden Museum (cat. ost. a).

4) Incomplete.

characterized by a gradual diminution of the ventral spine from the third to the sixth cervical vertebra. The spine on the third is very well developed, whereas the cervical vertebrae of *amphibius* possess much weaker ventral spines. Thus the difference between *siculus* and *sivalensis* is the same that exists between *amphibius* and *liberiensis*.

A distal part of a left radius was described by SEGUENZA (1907, p. 115, pl. V figs. 49-50) only as having "perfettamente conservate le superficie articolari". From these "very well preserved articulation surfaces", however, it is evident that this fragment does not belong to *sivalensis* (F.A.S., pl. 65 figs. 16, 16*c*, 18, 18*b*, 19, 19*a*, 20*a*, 20*b*, 33, and 33*b*), for in *siculus*, as in *amphibius*, the crest between the surfaces for articulation with scaphoid and with lunar is directed more antero-posteriorly, and the former surface is relatively smaller than in *sivalensis* and in *liberiensis*. Measurements are not given by SEGUENZA, but the scale of the figure, given as 1/3 nat. size, in all probability is 1/4 nat. size [1]), in agreement with another figure representing a radius and occurring on the same plate. The fine left radius and ulna of *hipponensis*, figured by STROMER (1905, pl. XX fig. 4) are figured in a way as to make a comparison with SEGUENZA's figures almost impossible; the surface for the articulation with the lunar is directed in the same way as in *amphibius* and, consequently, as in *siculus*.

Radius, distal part	*siculus*	*amphibius*		*hipponensis*	*liberiensis*
Transverse diam.	?ca. 90	107	117	69	48
Ant. post. diam.	?ca. 60	78	78	—	37

A "cuneiforme destro" (right cuneiform) (SEGUENZA, 1902, p. 165, pl. VII figs. 22-23) was stated to agree with the corresponding bone of *sivalensis* (F.A.S., pl. 65 fig. 26). However, both the figures of SEGUENZA and that in F.A.S. present an unciform and not a cuneiform [1]). Two differences are to be noted, viz., in *siculus* the surface for the articulation with the cuneiform is more concave than in *sivalensis*, and the surface for the articulation with the lunar (SEGUENZA, l.c., fig. 23 at the left) is relatively narrower than in *sivalensis* (F.A.S., pl. 65 figs. 26 and 26*a*, at the right). In these respects *siculus* agrees with *amphibius*, and *sivalensis* with *liberiensis*; unfortunately the figures make further comparison impossible, but for the rest *siculus* agrees with *amphibius* and not with *liberiensis* in the possession of a shallow and broad rough fossa behind the articulation surface for the cuneiform; and *sivalensis* agrees with *liberiensis* and not with *amphibius* in the more slender shape, and the presence of a distinct crest separating the facets for the 4th and 5th metacarpal respectively. The latter two *sivalensis-liberiensis* features are mentioned by STROMER (1914, p. 17) to occur in *hipponensis*; from his figure (l.c., fig. 8) it appears that the articulation surface for the lunar is narrower in comparison to that for the cuneiform, a feature in which *hipponensis* agrees with *siculus* and *amphibius*.

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[1]) A proximal part of a radius is figured on the same plate (SEGUENZA, 1907, pl. V figs. 53-54). In my opinion (see p. 319) this belongs to *Parabos* (?) spec. It has not escaped SEGUENZA's notice that the distal part of the radius did not fit well the proximal part (which he considers to belong to *Hippopotamus* too), for he states (l.c., p. 115) that the distal part "per le sue maggiori dimensioni" (on the evidence of its rather larger dimensions) must have belonged to "un individuo piu adulto" (an older individual). Supposing that the figure represents the bone on 1/3 nat. size, as stated by SEGUEZAN, the dimensions would not be larger, but even be smaller than those of the proximal part!

Unciform	*siculus*	*amphibius*		*sivalensis*	*hipponensis*	*liberiensis*
Ant. post. diam.	56	83	83	—	50 [2])	42.5
Ant. breadth	49	74	85	ca. 60	40	34
Max. height	49	44	45	ca. 40	22	26

Two left astragali of *siculus* are figured (SEGUENZA, 1902, pl. VII figs. 4-7 and 8-9 [3])). They differ considerably from *sivalensis* (F.A.S., pl. 66 figs. 20-24, pl. 68 figs. 20-21). In the Sicilian specimens nothing is to be seen of the well marked difference in level between the oblique facies articularis cuboidea and the facies articularis navicularis, so typical of the Asiatic hippopotami. The astragalus of *siculus* is broader and thicker than that of *sivalensis*, and the tuberosity below the medial ridge of the trochlea does not occur in *siculus*. The facies articularis calcanea posterior in *siculus* proximally is narrower than distally; in *siva-*

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[1]) SEGUENZA evidently is led astray by the incorrect designation of both cuneiform and unciform as "cuneiform" in FALCONER (1868 I, p. 504-505). The bones represented in F.A.S., pl. 65 figs. 19*h*, 21*h* and 26 are unciforms, as correctly stated by LYDEKKER (1885, p. 304).

[2]) Incomplete.

[3]) According to the text (l.c., p. 165) the former originates from Scirpi, the latter from Gravitelli; in the explanation of the plates (l.c., pp. 174-175), however, Gravitelli is mentioned as the locality for both.

lensis, in *liberiensis*, and often in *amphibius* the reverse is the case. In *siculus* there is a broad and shallow fossa medially of the facies articularis calcanea posterior.

The astragalus of *hipponensis*, figured by STROMER (1914, p. 19, figs. 11*a* and 11*b*), is intermediate between that of *siculus* and *sivalensis* as regards the difference in level between the facies articularis cuboidea and the facies articularis navicularis, and as regards the shape of the facies articularis calcanea posterior. In *hipponensis*, however, the bone is smaller and more slender than that of *siculus*, the fossa situated medially of the facies articularis calcanea posterior is narrower, and the lateral ridge of the trochlea is higher. *H. hipponensis* agrees with the Asiatic hippopotami in the presence of a tuberosity immediately below the medial ridge of the trochlea. The astragalus of *liberiensis* closely resembles that of the Asiatic hippopotami, viz., in the slender shape, in the well marked difference in level between the facies articularis cuboidea and the facies articularis navicularis, and in the prominent lateral ridge of the trochlea.

Astragalus	*siculus*		*amphibius*		*hipponensis*	*liberiensis*
Lateral length	102	97	105	106	ca. 85	53
Distal breadth	69	67	91	98	ca. 67	40
Ant. post. diam. (lateral)	57	54	59	60	ca. 48	26

The cranium of *hipponensis*, *pantanellii*, and *siculus* being still unknown, it is impossible to indicate the relationship between the known forms with any degree of certainty. In Asia, *Hippopotamus* appears first in the Dhok Pathan stage of the Siwaliks, correlated by PILGRIM (1913, pl. 26; 1931, p. 151; 1940, p. 11) with the Pontian of Europe. It is remarkable that the only Pontian species of *Hippopotamus* in Europe agrees with the Asiatic species in the upper C having a deep posterior groove. The same feature we met with only in the recent African *liberiensis*. As the skeletal features of this recent species bear a remarkably close resemblance to those of the Asiatic hippopotami, it seems improbable that genetical relations exist between *siculus* and *liberiensis*. On the other hand, the skeleton of *siculus* shows the greatest resemblance to *amphibius*. *H. hipponensis*, which is found together with *amphibius* in the Villafranchian of Algeria, differs more than *siculus* from *amphibius* in its skeletal characters, but differs less in its dentition, AIRAGHI (1921, p. 416) regards *pantanellii*, of which species only teeth are known, as ancestral to *amphibius;* from this form *pent-*

landi and *minor* should have originated. This is certainly unjustified; species with complicated molars cannot be regarded as intermediate between *pantanellii* and *minor*, which resemble each other in the primitive molar structure.

A rather puzzling species is *liberiensis*, which is regarded as a pigmy form of *amphibius* by some authors, e.g., AIRAGHI (l.c., p. 417); this is not confirmed, however, by the skeletal characters. From the evidence that in *lemerlei* (JOLEAUD, 1920, p. 14) the I_1 and in *amphibius* (JOLEAUD, 1921, p. 20) the id_1 are developing first, JOLEAUD thinks that a diprotodont unknown form in the Burdigalian of Africa must have been ancestral to both. His speculations are based upon a fragment of a mandibular symphysis from the Aquitanian of Baluchistan, originally identified by FORSTER-COOPER (1915) as *Aprotodon smithwoodwardi*, and supposed to be a hippopotamus. Later VAUFREY (1928, p. 231, see figs. 1 and 2), however, referred the fragment to the rhinoceroses as *Chilotherium* spec. JOLEAUD's speculations have already been criticized by DEPÉRET (1921).

Taking into consideration all the facts gathered above one must admit that we are still far from being able to indicate the relations between the African and European Hippopotamidae, of which the pre-Pontian history is unknown.

Parabos (?) spec.

SEGUENZA (1907, p. 115, pl. V figs. 53-54) referred to *Hippopotamus sivalensis* Falconer et Cautley a proximal part of a right radius. The bone is only described as being "abbastanza ben conservato e le superficie articolari sono intatte" (sufficiently well preserved, the articulation surfaces intact). From the figures (their scale is mentioned as 1/3 nat. size, from the measurements given in the text it is, however, evident that they are on 1/4 nat. size) it appears that the bone belongs to a bovid. This is evident from the even thickness of the corpus radii, from the lesser broadening of the capitulum radii, and from the difference between the antero-posterior diameter of the medial and that of the lateral part of the facies articularis humeralis being much less pronounced.

The Bovidae in the Gravitelli fauna are identified by SEGUENZA as *Gazella deperdita* (Gervais), *Antilope* spec. and *Tragocerus* spec. The radius, however, is too large to belong to one of these forms, and agrees in size and in a typical feature, viz., the lack of a tuberositas proximalis lateralis, with the radius of *Parabos macedoniae* Arambourg et Piveteau from the Pontian of Salonica, as figured by ARAMBOURG and PIVETEAU (1929*b*, pl. IX fig. 3). These authors describe the radius as having "la tuberosité externe presque nulle" (l.c., p. 62); the proximal width is 75 mm (l.c., p. 63), whereas the measurements of the Gravitelli radius are: proximal width 73 mm, antero-posterior diameter 52 mm. *Parabos boodon* (Gervais) from Roussillon is of about the same size; the proximal width of the radius is 69 mm (DEPÉRET, 1890, p. 95). PILGRIM (1939*a*, p. 278), however, doubts if *macedoniae* belongs to the genus *Parabos* 1). For the great resemblance of the radius from Gravitelli to that of *macedoniae*, I identify the bone as *Parabos* (?) spec.

Dicerorhinus (?) spec.

Before dealing with the rhinoceros remains described and figured by SEGUENZA as *Hippopotamus sivalensis* Falconer et Cautley it is desirable to check SEGUENZA's identification of the tooth which that author indeed recognized as belonging to a rhinoceros, viz., a "penultimo molare superiore di sinistra" (upper left penultimate molar) (SEGUENZA, 1902, pp. 167-168, pl. VI figs. 9-11). It is identified by SEGUENZA as "*Rhinoceros* (*Dihoplus*) *Schleiermacheri* Kaup". Up to 1921 two species have been confused under the name *schleiermacheri*, viz., the species from the typical locality Eppelsheim, and a species from Pikermi and Samos. This has been indicated by SCHLOSSER (1921), who referred the Pikermi and Samos specimens to a var. *orientalis*. RINGSTRÖM (1924) fully discusses the cranial differences between the true *schleiermacheri* and *orientalis*, and states that they possess an "äusserst ähnlichen Zahnbau" (l.c., p. 18). To *orientalis* he refers also material from China.

The crown portion figured by SEGUENZA is not much worn. It has a moderately developed paracone style, becoming vaguer towards the base. A very slight median tumefaction occurs on the

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1) The genus *Parabos* has been established by ARAMBOURG and PIVETEAU (1929*a*, p. 145) to include *Palaeoryx boodon* (Gervais) and *Palaeoryx cordieri* (Christol), as these species differ in cranial features from the typically Pontian *Palaeoryx* (viz., *P. pallasii* (Wagner) and *P. majori* Schlosser) as well as from the recent *Hippotragus*; they seem to be more closely related to the Bovinae. The skull of *macedoniae* being not known, its reference to the genus *Parabos* is not certain.

outer surface. The posterior half of the outer surface is more inclined than the anterior and bears a metacone style, which is more defined anteriorly than posteriorly. The metastyle is rather prominent posteriorly. The anterior cingulum forms a distinct ledge and is somewhat crenulated. It is especially raised from the surface in its lingual third; above this part the protoloph has a vertical groove. The cingulum seems not to pass round the protoloph but to end at the antero-internal angle (this part of the tooth is damaged). The medisinus seems to be comparatively wide, the metaloph gives off a large crochet which projects about the whole way across the medisinus. It stands at a little more than right angle to the metaloph and is bounded lingually by a groove. The shape of the portion of the medisinus labially of the crochet and that of the postsinus is not clear from the figures.

This tooth is much smaller than the second upper true molar of *Dicerorhinus schleiermacheri* (Kaup) and of *Dicerorhinus orientalis* (Schlosser). Its breadth is only 47 mm, whereas the breadth of M^2 in *schleiermacheri* is 65 mm (KAUP, 1834, pp. 35, 37) and in *orientalis* varies from 62.5 to 71 mm (WEBER, 1903, p. 495). The breadth of an M^2 of *orientalis* from China is 63 mm (RINGSTRÖM, 1924, p. 13). The dimensions of the Gravitelli tooth are in agreement with those of the pd^4 of these species. The pd^4 from Eppelsheim figured as *schleiermacheri* by KAUP (1834, Atlas, pl. XI fig. 7) differs from the Gravitelli specimen in the absence of a metacone style, the presence of an antecrochet and in the crochet being directed parallel to the outer surface. I doubt, however, if the Eppelsheim milk dentition really belongs to *schleiermacheri*, for it has a very great resemblance to the milk dentition from Samos, figured by WEBER (1903, pl. XIV fig. 1) which is stated by RINGSTRÖM (1924, p. 23) to belong probably to *Diceros pachygnathus* (Wagner) and not to *schleiermacheri*. Another pd^4 from Eppelsheim referred to *schleiermacheri* by KAUP (1843, Atlas, pl. XII fig. 3), which is stated to be "mieux formée" (l.c., p. 36) has a tumefaction above the posterior root, only a weak antecrochet and a shorter crochet almost at a right angle to the metaloph.

The Gravitelli tooth agrees with the pd^4 from Samos, figured as *pachygnathus* by WEBER (1903, pl. XVI fig. 2) but identified as *orientalis* by RINGSTRÖM (1924, p. 23), in the presence of a metacone style and of a vertical groove in the anterior surface of the protoloph; in the slight difference between the antero-transverse and postero-transverse diameter; in the absence of an antecrochet and (probably) of the lingual cingulum. In the pd^4 of *orientalis* from China (Ringström, 1924, pl. I figs. 1-2) the metacone style has not developed; these teeth, except for their larger size, present no differences from the pd^4 from Pikermi, figured as *pachygnathus* by Gaudry (1862-67, Atlas, pl. XXIV fig. 1) and referred to *orientalis* by Ringström (1924, p. 22).

With regard to the great variation of the milk premolars within the species it seems best to indicate the Gravitelli tooth as *Dicerorhinus* (?) spec.

	(?) species	*schleiermacheri*		*orientalis*				
pd^4	Seguenza, 1902, p. 167	Kaup, 1834, p. 36	p. 37	Weber, 1903, p. 489			Ringström, 1924, p. 13	
	Gravitelli	Eppelsheim		Pikermi		Samos	China	
Length	56	48	51	45	47	52-58	54	55
Anterior breadth	47	48	52	45	45	41-45	49	50
Posterior breadth	44	—	—	—	—	—	—	—

Diceros aff. *pachygnathus* (Wagner)

Three bones, which Seguenza in his second paper referred to *Hippopotamus sivalensis* Falconer et Cautley, belong to a rhinoceros:

1. The proximal part of a left scapula (Seguenza, 1907, p. 115, pl. VI figs. 12-13). The cavitas glenoidalis is almost entire, the tuber scapulae has broken off. The cavitas glenoidalis, broader in its posterior part, is more rounded than in *Hippopotamus*, and has a thin and sharp border, only somewhat thickened anteriorly. Both on the lateral and on the costal surface, anterior to the cavitas glenoidalis, a distinct fossa is seen, of which that on the lateral surface is larger proximally and extends more anteriorly than that on the costal surface. The latter fossa is visible in fig. 13 because the processus coracoideus is broken off.

2. A left unciform (Seguenza, 1907, p. 115, pl. V figs. 51-52) belongs to a rhinoceros too, as appears from the following facts: The posterior elongation is much longer and more slender (the bone is "completo e ben conservato" (complete and well preserved)), the facies articularis lunaris is much more oblique, immediately below the latter the bone is deeply concave, the facies articularis for the cuneiform is flat instead of concave, the facet for the 5th metacarpal is much smaller. The unciform is much higher than that of *Hippopotamus*, the lateral part is higher than the medial instead of the reverse. The articulation surface for the cuneiform does not extend to the lateral margin of the bone, it

meets the articulation surface for the lunar, and the latter meets the anterior surface at much less obtuse angles than in *Hippopotamus*.

3. The distal part of a left second metacarpal (SEGUENZA, 1907, p. 116, pl. VI figs. 21-22) belongs to a rhinoceros. This is evident from the presence of a distinct lateral tuberosity, situated somewhat more proximally than the less developed but broader medial tuberosity, and from the shape of the distal articulation surface. In the latter the facet for the lateral sesamoid bone is more prominent than the broader one for the medial sesamoid bone; on the anterior surface both the medial and the lateral part are rounded off gradually; on the posterior surface it is seen to be more prominent than in *Hippopotamus*.

These three bones in all respects, except their smaller size, agree with *Diceros bicornis* (L.). The scapula differs from *Dicerorhinus sumatrensis* (Fischer), from *Dicerorhinus hundsheimensis* (Toula) (1902, pl. VI fig. 1*c*), and from *Dicerorhinus caucasicus* Borissiak (1938, p. 22, fig. 3*c*) in the relatively broader cavitas glenoidalis. The unciform differs from *Dicerorhinus sumatrensis* (Fischer), from *Dicerorhinus schleiermacheri* (Kaup) (1834, Atlas, pl. XIII figs. 8 and 8*a*; 1854, pl. 7 fig. 6), from *Dicerorhinus hundsheimensis* (Toula) (1902, pl. VIII fig. 1), and from *Dicerorhinus caucasicus* Borissiak (1938, p. 31, figs. 8*a* and 8*c*) in the more obtuse angle between the articulation surfaces for the lunar and for the cuneiform (in *hundsheimensis* this angle is even acute). Compared with *sumatrensis*, *schleiermacheri*, and *hundsheimensis* the Sicilian fossil is relatively less high (the unciform of *caucasicus* is damaged at the lower border of its anterior surface). The unciform of *Diceros pachygnathus* (Wagner), only an anterior view of which is represented by GAUDRY (1862-67, Atlas, pl. XXVIII fig. 5, lower side at the right), agrees with the Sicilian bone and *Diceros bicornis* (L.). The metacarpal differs from *Dicerorhinus sumatrensis* (Fischer), and from *Dicerorhinus schleiermacheri* (Kaup) (1854, pl. 7 fig. 4, pl. 9) in the less convex distal articulation surface (not represented in the figures of *Dicerorhinus hundsheimensis* (Toula) (1902, pl. VII fig. 5, pl. VIII fig. 1), of *caucasicus*, and of *Diceros pachygnathus* (Wagner) (GAUDRY, 1862-67, Atlas, pl. XXVIII fig. 6)).

In the table on p. 324 the measurements of the Gravitelli bones can be compared with those of *Diceros bicornis* (L.) and with those of *Diceros pachygnathus* (Wagner) from Pikermi. GAUDRY (1878, p. 45) states: "... le rhinocéros bicorne d'Afrique a une étonnante ressemblance avec le *Rhinoceros pachygnathus* de Pikermi." Unfortunately the measurements of the corresponding bones of *Diceros pachygnathus* (Wagner) from Samos are not mentioned by Weber (1903). Therefore, the measurements of other bones of the anterior extremity are listed too. Mostly the measurements of the bones of *pachygnathus* fall into the range of variation observed in only four specimens of *bicornis*; in a few instances the bones from Pikermi and Samos are larger, those from the former locality sometimes are smaller in one dimension than *bicornis*. The Gravitelli bones, however, in all dimensions are smaller than *bicornis*; they may not be identical with *pachygnathus*, but certainly have affinities to this species. Therefore I identify the Sicilian specimens as *Diceros* aff. *pachygnathus* (Wagner).

	pachygnathus			*bicornis*			
	Gravitelli	Pikermi Gaudry, 1862-67	Samos Weber, 1903	Gaudry, 1862-67	Leiden Mus. cat. *a*	Leiden Mus. cat. *f*	Zool. Mus. Amsterdam no. 506
Scapula: cav. glen. ant. post.	82	105	—	108	95	92	101
Id., transverse diam.	77	80	—	96	87	82	91
Radius: length	—	353	380	390	386	355	387
Id., prox. breadth	—	115	122	119	112	105	122
Id., distal breadth	—	117	116	117	106	103	107
Ulna: length	—	450	500	480	498	455	515
Id., ant. post. middle of corp.	—	42	49	41	42	42	35
Id., distal breadth	—	50	50	50	68	63	70
Scaphoid: vert. diam.	—	68	62	—	63	52	63
Id., transv. diam.	—	87	88	—	82	75	86
Lunar: ant. post. diam.	—	77	79	—	75	67	78
Id., transv. diam.	—	60	62	—	52	46	57
Magnum: ant. post. diam.	—	100	100	—	97	88	98
Id., transv. diam.	—	45	71	—	53	47	64
Unciform: vert. diam.	43	58	—	—	57	50	61
Id., ant. post. diam.	79	96	—	—	100	85	107
Id., transv. diam.	63	67	—	—	75	64	79
Metacarpal II length	—	147	—	150	160	145	171
Id., distal breadth	42	52	—	44	46	44	45
Metacarpal III length	—	166	—	172	190	174	205
Id., distal breadth	—	75	78	75	72	65	78
Metacarpal IV length	—	128	138	135	152	139	163
Id., distal breadth	—	51	55	50	50	49	53

Incertae sedis

I am not certain about the "canini inferiori di giovane individuo" (lower canini of a young individual) (Seguenza, 1902, p. 164, pl. VII figs. 15-19), and about the "premolare di latte" (milk premolar) (Seguenza, 1907, pl. VII fig. 21), which have been referred by Seguenza to *Hippopotamus sivalensis* Falconer et Cautley. The "canini" certainly did not belong to a young animal, for they are of an even thickness over their whole length. Both teeth are curved; they have a distinct longitudinal groove along the inner curve. In the smaller of the two (l.c., figs. 15-17) a less distinct longitudinal groove is present along the outer curve; one of its sides is flat, the other is convex. The short abrasion surface is situated at the inner curve; it shows transverse scratches. In the larger tooth (l.c., figs. 18-19) the outer curve is flat; this tooth is less compressed than the smaller, and both its sides are convex. In his second paper on the Gravitelli fauna, Seguenza (1907, p. 110) mentions another canine of a young specimen; unfortunately this tooth is not figured. The measurements in mm are as follows:

	length	greater diameter	smaller diameter
Seguenza, 1902, p. 164, pl. VII figs. 15-17	78	26	20
Seguenza, 1902, p. 164, pl. VII figs. 18-19	116	22	19
Seguenza, 1907, p. 110	(54)	24.5	19

The specimens do not belong to a hippopotamus. One of them has been referred to a rhinoceros by Natale (Ricerche geognostiche dei dintorni di Messina. Messina, 1851, p. 54, non vidi, fide Seguenza, 1902, pp. 118, 124, 164). However, I do not know a rhinoceros in which the lower tusks present the same cross section.

Neither does the supposed milk premolar belong to *Hippopotamus*. As judged from the only figure given, it is merely a fragment; its breadth is given as 22 mm.

The present paper may give rise to further researches on the mammalian fauna from Gravitelli. New collections must be made. The fauna seems to be almost forgotten, since it is not mentioned in many recent papers in which one might expect to find it. The Proboscidea (if Seguenza's identifications are correct, both *Mastodon* (*Zygolophodon*) *turicense* Schinz and *Mastodon* (*Zygolophodon*) *borsoni* Hays occur in the Gravitelli fauna!), e.g., are not mentioned by Osborn (1936). Pilgrim, who in another instance (see p. 301) mentions the Carnivora from Gravitelli, however, derogates himself in overlooking the Gravitelli *Hippopotamus*, when dealing with MATTHEW's and COLBERT's hypothesis, that the Dhok Pathan stage of the Siwaliks is to be correlated with the European Astian. PILGRIM (1939*b*, p. 457) states the *Hippopotamus*, as being in both regions an invading form, to occur first in Casino and Wadi Natrun. If the first known appearance in Europe and in Asia of a genus of unknown origin is of any correlation value, the Gravitelli *Hippopotamus* on the contrary strengthens PILGRIM's view that the Dhok Pathan is equivalent to the Pontian of Europe.

It may be convenient to the reader to give below a new explanation of the plates belonging to SEGUENZA's papers, as far as concerns the material which has incorrectly been referred by this author to *Hippopotamus sivalensis* Falconer et Cautley.

Boll. Soc. Geol. Ital., vol. XXI, 1902

Plate VII

Figs. 1-3, *Hippopotamus siculus* Hooijer, fragment of left maxillary with pd^3 (roots), pd^4, and M^1; fig. 1 labial view, fig. 2 lower view, fig. 3 lingual view (S. Pier Niceto).

Figs. 4-7, *Hippopotamus siculus* Hooijer, left astragalus; fig. 4 anterior view, fig. 5 lateral view, fig. 6 medial view, fig. 7 posterior view (Scirpi or Gravitelli).

Figs. 8-9, *Hippopotamus siculus* Hooijer, left astragalus; fig. 8 lateral view, fig. 9 posterior view (Gravitelli).

Figs. 10-11, *Hippopotamus siculus* Hooijer, fragment of left M^2; fig. 10 labial view, fig. 11 lower view (Gravitelli).

Figs. 12-14, *Hippopotamus siculus* Hooijer, upper C; fig. 12 section of left specimen, fig. 13 median view of right idem, fig. 14 section of the latter (Gravitelli).

Figs. 15-19, incertae sedis (Gravitelli).

Fig. 20, *Hippopotamus siculus* Hooijer, left pd^4(?), anterior view (S. Pier Niceto).

Fig. 21, incertae sedis (Gravitelli).

Figs. 22-23, *Hippopotamus siculus* Hooijer, right unciform; fig. 22 posterior view, fig. 23 upper and somewhat anterior view (Gravitelli).

Figs. 1-3, and 10-21 nat. size; figs. 4-9, 22 and 23 1/2 nat. size.

Boll. Soc. Geol. Ital., vol. XXVI, 1907

Plate V

Figs. 49-50, *Hippopotamus siculus* Hooijer, distal part of left radius; fig. 49 anterior view, fig. 50 distal view (Gravitelli).

Figs. 51-52, *Diceros* aff. *pachygnathus* (Wagner), left unciform; fig. 51 upper view, fig. 52 anterior view (Gravitelli).

Figs. 53-54, *Parabos* (?) spec., proximal part of right radius; fig. 53 anterior view, fig. 54 proximal view (Gravitelli).

Figs. 49-50 (?) 1/4 nat. size; figs. 51-52 1/2 nat. size; figs. 53-54 1/4 nat. size.

Plate VI

Figs. 1-3, *Hippopotamus siculus* Hooijer, fragment of right mandibular ramus with unworn M_1 and erupting M_2; fig. 1 labial view, fig. 2 upper view, fig. 3 lingual view (Gravitelli).

Figs. 4-6, *Hippopotamus siculus* Hooijer, third vertebra cervicalis; fig. 4 ventral view, fig. 5 caudal view, fig. 6 cranial view (Gravitelli).

Figs. 7-8, *Hippopotamus siculus* Hooijer, right M^3; fig. 7 lingual view, fig. 8 lower view (Gravitelli).

Figs. 9-10, *Hippopotamus siculus* Hooijer, right M^1; fig. 9 lingual view, fig. 10 lower view (Gravitelli).

Fig. 11, *Hippopotamus siculus* Hooijer, upper left C, median view (Gravitelli).

Figs. 12-13, *Diceros* aff. *pachygnathus* (Wagner), proximal part of left scapula; fig. 12 lateral view, fig. 13 proximal view (Gravitelli).

Figs. 14-15, *Hippopotamus siculus* Hooijer, left pd_3; fig. 14 lingual view, fig. 15 upper view (Gravitelli).

Fig. 16, *Hippopotamus siculus* Hooijer, right pd_3, labial view (Gravitelli).

Figs. 17-18, *Hippopotamus siculus* Hooijer, left P^2; fig. 17 lingual view, fig. 18 lower view (Gravitelli).

Figs. 19-20, *Hippopotamus siculus* Hooijer, left pd_2; fig. 19 lingual view, fig. 20 upper view (Gravitelli).

Figs. 21-22, *Diceros* aff. *pachygnathus* (Wagner), distal part of left 2nd metacarpal; fig. 21 posterior view, fig. 22 anterior view (Gravitelli).

Figs. 1-11, and 14-22 1/2 nat. size; figs. 12-13 1/3 nat. size.

Plate VII

Figs. 1-2, *Hippopotamus siculus* Hooijer, right M_2 and M_3; fig. 1 labial view, fig. 2 lingual view (Gravitelli).

Figs. 3-4, *Hippopotamus siculus* Hooijer, right M_1; fig. 3 labial view, fig. 4 upper view (Gravitelli).

Figs. 5-6, *Hippopotamus siculus* Hooijer, right P_2; fig. 5 lingual view, fig. 6 upper view (Gravitelli).

Figs. 7-8, *Hippopotamus siculus* Hooijer, right P_3; fig. 7 lingual view, fig. 8 upper view (Gravitelli).

Figs. 9-10, *Hippopotamus siculus* Hooijer, left P^4; fig. 9 labial view, fig. 10 lower view (Gravitelli).

Figs. 11-12, *Hippopotamus siculus* Hooijer, lower right C; fig. 11 lateral view, fig. 12 upper view (Gravitelli).

Fig. 13, *Hippopotamus siculus* Hooijer, I_1 (Gravitelli).

Figs. 14-15, *Hippopotamus siculus* Hooijer, lower or upper I, two specimens (Gravitelli).

Fig. 16, *Hippopotamus siculus* Hooijer, (?) I^2 (Gravitelli).

Figs. 1-10, and 13-16 1/2 nat. size; figs. 11-12 1/3 nat. size.

Note. Since the above article was written, I exchanged letters and papers with Miss DOROTHEA M. A. BATE in London and with Prof. C. ARAMBOURG in Paris, which make the following additions necessary:

Miss BATE sent me the paleontological part of "The Stone Age of Mount Carmel. Excavations at the Wady El-Mughara" (Oxford, Clarendon Press, 1937). *Hippopotamus amphibius* (l.c., p. 200/201) was contemporaneous with primitive man in the Upper Acheulean of Tabūn and the Lower Levalloiso-Mousterian of Tabūn and Skhūl in Palestine. The species has been recorded too from Syria and Palestine, viz., from Sidon and the Zuttiyeh Cave. As far as my knowledge goes, these are the only records of the species being found outside Europe and Africa.

Prof. ARAMBOURG (C. R. Acad. Sci. Paris, vol. 218, 1944, pp. 602-604) refers the Omo hippopotamus to a new species, *H. protamphibius*. An elaborate memoir on the Omo fauna will be published before long in the "Mission scientifique de l'Omo". Prof. ARAMBOURG sticks to the original opinion of GAUDRY as to the hexaprotodont character of *Hippopotamus hipponensis* (Bull. Soc. Géol. France, ser. 5, vol. 14, 1944, pp. 147-153, pl. III), and regards the Astian hippo from Wadi Natrun as a subspecies of his *H. protamphibius*. The record of *Hippopotamus imaguncula* Hopwood from the Omo fauna (ARAMBOURG, 1934, p. 307) is based on specimens of *H. protamphibius;* to the latter species also belong the remains which JOLEAUD (1920, p. 22) regarded as not different from *H. amphibius*. A new record of *H. imaguncula* Hopwood is that from the Pleistocene Kanam and Rawe beds, N. of Homa Mountain in Kenya (KENT, Geol. Mag., vol. 79, 1942, pp. 120, 124).

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HYDROIDEN UIT DE WADDENZEE

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In den loop van 1937 en 1938 werden door Dr. J. Verwey en een aantal medewerkers Hydroiden verzameld gedurende onderzoekingstochten in de Waddenzee die voornamelijk ten doel hadden een kartographische opname van de fauna te maken. Het Hydroiden materiaal werd eerst aan Dr. P. Wagenaar Hummelinck verzonden, die echter geen tijd kon vinden om het te bewerken en zoo vriendelijk was mij de collectie ter hand te stellen. Hoewel de verzameling niet uitgebreid genoemd kan worden, is zij toch faunistisch van vrij groote waarde, omdat van verspreiding en voorkomen der Hydroiden in de Waddenzee zeer weinig bekend is. De Hydroidenfauna van de haven en de onmiddellijke omgeving van Den Helder is ten gevolge van het geregelde verzamelen door de talrijke bezoekers van het Zoölogisch Station vrij volledig bekend. Voorkomen en verspreiding van de aldaar aangetroffen Hydroiden zijn besproken door verschillende auteurs (cf. Vosmaer, 1878; Horst, 1881; Funke, 1918; Van der Sleen, 1920; Van Benthem Jutting, 1922; Hummelinck, 1930). Funke (1922) en Hummelinck (1936) hebben bovendien het voorkomen van Hydroiden in het voormalige Zuiderzeegebied behandeld, voordat dit gebied door de afsluiting in Mei 1932 zijn waarde als vindplaats van mariene Hydroiden geheel verloor. Tot op heden is er echter nog geen enkele mededeeling gedaan over het voorkomen van Hydroiden in de Waddenzee. De hier besproken soorten zijn ten deele van den bodem gedregd met behulp van een trawlnet; voor een ander, niet minder belangrijk deel werden zij met behulp van een bodemhapper boven gebracht. Nauwkeurige opgaven betreffende de vindplaatsen en de diepte waarop werd verzameld zijn te vinden in het onderstaande „Overzicht van vindplaatsen en materiaal”. De zeer nauwkeurige opgaven van de vindplaatsen zijn niet steeds herhaald bij de bespreking der soorten, maar zijn daar verkort weergegeven. Alle plaatsen waarop in den loop van het onderzoek door Dr. J. Verwey materiaal werd verzameld zijn door hem in kaart gebracht; de betreffende kaarten berusten in het Zoölogisch Station te Den Helder, dat tijdelijk ondergebracht was in het Rijksmuseum van Natuurlijke Historie te Leiden. De vangsten verkregen met behulp van bodemhappers en trawlnet zijn genummerd, deze nummers zijn eveneens in het onderstaande overzicht vermeld; de trawlnet-vangsten zijn bovendien te vinden op de kaart in het artikel van Verwey (1942, fig. 1). Een uitzondering is gemaakt voor *Hydractinia echinata* (Flem.). Deze hydropolyp is in vrijwel alle trawlnetvangsten aangetroffen, hoofdzakelijk op Gastropodenschelpen bewoond door *Pagurus bernhardus* (L.). Over het geheele Waddenzeegebied tot dicht onder den afsluitdijk komt zij algemeen voor; zij is aangetroffen in Marsdiep, Malzwin, Wierbalg, Vlieter, Texelstroom, Scheurrak, Omdraai, Inschot, Zuidoostrak, Slenk, Schuitengat, Noordmeep en Oostmeep. Aangezien van *Hydractinia* geen materiaal apart gehouden is blijft zij hier verder buiten beschouwing; de overige Hydroiden zijn opgenomen in de collectie van het Zoölogisch Museum te Amsterdam.

Wanneer in het onderstaande gesproken wordt over den mond van de Zuiderzee dan is hiermee bedoeld een strook van de Zuiderzee die doorsneden wordt door de lijn Wieringen-Kornwerderzand.

De systematische rangschikking der soorten is zooveel mogelijk in overeenstemming met de opvattingen van Broch, wiens zorgvuldige onderzoekingen over de variabiliteit en de verspreiding der boreale Hydroiden de basis vormen voor ieder, die zich met de Noordzee-Hydroiden wil bezighouden.

OVERZICHT VAN VINDPLAATSEN EN MATERIAAL

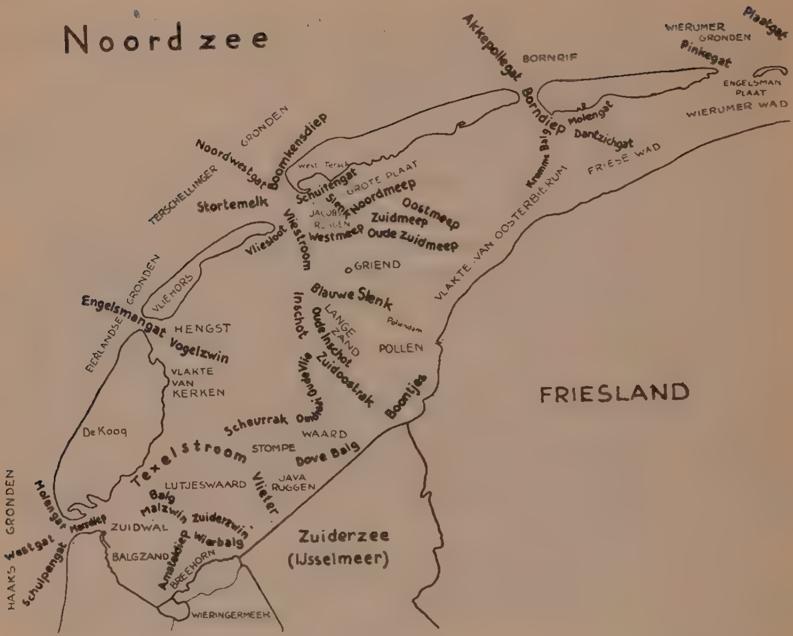
Blauwe Slenk, 30 Aug. 1937, no. 137, diepte 15 m (geëtiketteerd: XV, Blauwe Slenk, tusschen zwarte lichtboei no. 8 en roode ton no. 5): *Laomedea dichotoma* (L.).

Vliestroom, 25 Aug. 1938, no. 205, diepte 27 m (geëtiketteerd: II, Vliestroom, tusschen bolton S.B.d.O. en roode ton no. 6 van Stortemelk, op 1/3 afstand vanaf de eerste: *Campanulina* cf. *lacerata* (Johnst.), *Laomedea dichotoma* (L.).

Vliestroom, 25 Aug. 1938, no. 206, diepte 23 m (geëtiketteerd: III, Vliestroom, tusschen hoekton S.B.d.O. en roode ton no. 6 van Stortemelk, op 2/3 afstand vanaf de eerste): *Sertularia cupressina* L., *Laomedea dichotoma* (L.).

Vliestroom, 25 Aug. 1938, no. 207, diepte 22 m (geëtiketteerd: IV, Vliestroom, bij roode ton no. 6 van Stortemelk): *Laomedea* spec.

Oostmeep, 26 Aug. 1938, no. 240, diepte 13 m (geëtiketteerd: IV, Oostmeep, dwars van roode ton no. 9, 150 m vanaf de ton): *Laomedea longissima* (Pall.).



Westmeep, 26 Aug. 1938, no. 247, diepte 15 m (geëtiketteerd: XI. Westmeep, dwars van zwarte ton no. 2): *Laomedea dichotoma* (L.).

Westmeep, 26 Aug. 1938, no. 249, diepte 18 m (geëtiketteerd: XIII, dwars van zwarte ton no. 2, aan de zuidzijde van het vaarwater, en XIII, Westmeep): *Laomedea dichotoma* (L.); *Laomedea neglecta* Ald., *Laomedea gelatinosa* (Pall.).

Slenk, 29 Aug. 1938, trek 108 * + 109*, diepte 7–18 m (geëtiketteerd: Slenk, trek 2 + 3): *Tubularia* cf. *larynx* Ell. & Sol., *Laomedea longissima* (Pall.), *Laomedea dichotoma* (L.).

Oostmeep, 29 Aug. 1938, trek 100 * + 111 *, diepte 11–21 m (geëtiketteerd: Oostmeep, trek 4 + 5): *Calicella syringa* (L.); *Sertularia cupressina* L. *Campanularia johnstoni* Ald., *Laomedea longissima* (Pall.).

Schuitengat, 30 Aug. 1938, trek 113 + 115, diepte 10.5–12 m (geëtiketteerd: Schuitengat, trek I + II): *Tubularia* cf. *larynx* Ell. & Sol., *Bougainvillia ramosa* (Wright), *Calicella syringa* (L.), *Sertularia cupressina* L., *Campanularia johnstoni* Ald., *Laomedea dichotoma* (L.), *Laomedea geniculata* (L.), *Laomedea longissima* (Pall.).

Kornwerderzand, 29 Sept., 1938, no. 372, diepte 4.60 m (geëtiketteerd: XIX, Kornwerderzand, hap no. 372:) *Laomedea longissima* (Pall.), *Laomedea dichotoma* (L.), *Laomedea neglecta* Ald.

Kornwerderzand, 29 Sept. 1938, no. 373, diepte 5.70 (geëtiketteerd: XX, Kornwerderzand, hap no. 373): *Laomedea dichotoma* (L.), *Laomedea neglecta* Ald.

Kornwerderzand, 30 Sept. 1938, no. 393, diepte 5.50 m (geëtiketteerd:

XV, Kornwerderzand, hap no. 393): *Tubularia* cf. *larynx* Ell. & Sol., *Bougainvillia ramosa* (Wright), *Cuspidella costata* Hincks, *Campanularia johnstoni* Ald., *Laomedea dichotoma* (L.).

Tubularia cf. *larynx* Ellis & Solander, 1786 [1])

Slenk, 29 Aug. 1938, trek 108 * + 109 *. Enkele ± 7 cm hooge kolonies waarvan alleen de hydrocauli bewaard zijn gebleven.

Schuitengat, 30 Aug. 1938, trek 113 + 115. Verschillende ± 5 cm hooge kolonies, waarvan alleen de ledige hydrocauli behouden zijn gebleven.

Kornwerderzand, 30 Sept. 1938, no. 393. Een jong individu bevestigd op den hydrocaulus van *Bougainvillia ramosa* (Wright).

Van *Tubularia larynx* zijn geen goed ontwikkelde exemplaren in de verzameling aanwezig. De ledige hydrocauli van de Slenk en het Schuitengat, die zeer waarschijnlijk tot deze soort behooren, kunnen ook door zeestroomingen aangevoerd zijn, daar deze kolonies niet op een of ander vast voorwerp bevestigd waren en er geen sporen van coenosark of hydranthen meer te bekennen zijn. Jonge individuen van deze soort zijn beschreven als *Vorticlava humilis* Alder, 1856, *V. proteus* Wright, 1863, en *Acharadria larynx* Wright, 1863 (cf. BRINK, 1925). Het jonge exemplaar van Kornwerderzand komt goed overeen met de afbeeldingen van jonge polypen van *T. larynx*, welke door BRINK (1925, pl. 7 fig. 5) zijn gegeven. De jonge individuen van *T. indivisa* Linnaeus, 1758, welke soort eveneens in grooten getale langs de Nederlandsche kust voorkomt, zijn nog niet nauwkeurig afgebeeld of beschreven; BROCH (1937) is bovendien de meening toegedaan dat de door BRINK besproken *Vorticlava*- en *Acharadria*-polypen ontwikkelingsstadia van *Corymorpha annulicornis* M. Sars, 1859, zijn, welke opvatting echter zeer te betwijfelen is. *C. annulicornis*, een modder bewonende soort, is tot op heden alleen van de omgeving van Bergen, de Firth of Clyde en Plymouth bekend (cf. REES, 1938), terwijl de *Vorticlava*- en *Acharadria*-polypen in groote hoeveelheden tusschen *Tubularia*- en *Laomedea*-kolonies in de haven van Den Helder gevonden worden, waar *Tubularia larynx* buitengewoon talrijk is. *T. larynx* is vóór 1932 nooit in den mond van de Zuiderzee gevonden, zij komt nu echter in vrij groote hoeveelheden langs den noordkant van Wieringen voor. Kolonies van *T. larynx* spoelen gedurende het geheele jaar langs het geheele

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[1]) *Tubularia* kolonies zijn bovendien aangetroffen in het Oude Vlie (Oude Vlie, 30 Juli 1939, no. 461, dwars van roode ton no. 17 aan de noordzijde van het vaarwater) op een klomp veen en in het Schuitengat (trek 124, Schuitengat, 31 Juli 1939, tusschen zwarte ton no. 4 en hoekton, diepte 2–12 m).

Nederlandsche Noordzeestrand aan, varieerend van versche kolonies tot vrijwel ledige hydrocauli, zoodat deze soort zeer waarschijnlijk ook vlak voor de Nederlandsche Noordzeekust levend voorkomt. *T. indivisa* komt in zeer groote hoeveelheden voor langs de zuidelijke dijken van Schouwen en in geringer aantal ook in de haven van Den Helder. Levende of meer of minder vergane kolonies van die soort worden zoo nu en dan ook aangespoeld langs het Noordzeestrand aangetroffen.

Bougainvillia ramosa (Wright, 1858)

Schuitengat, 30 Aug. 1938. Een groot aantal tot ± 12 mm hooge kolonies op algen. Jonge gonophoren zijn aanwezig.

Kornwerderzand, 30 Sept. 1938, no. 393. Verschillende jonge, tot ± 8 mm hooge kolonies op *Fucus* en *Ceramium*. Geen gonophoren. Op één van de hydrocauli een jonge polyp van *Tubularia larynx* Ell. & Sol.

De *Bougainvillia*-kolonies van het Schuitengat komen goed overeen met de beschrijving van de forma *benedeni* Bonnevie, 1898 (cf. Brink, 1925). Een groot aantal schizosporen komt over alle kolonies verdeeld voor, de gonophoren zijn bevestigd aan den hoofdstam en aan de vertakkingen, zij vertoonen verschillende ontwikkelingstoestanden. Het periderm is gegolfd en vertoont alleen aan de bases der takjes een paar duidelijke ringen. De steriele kolonies van het Kornwerderzand hebben monosiphone hydrocauli, die zich verheffen van een onregelmatige en verwarde massa hydrorhizadraden. Zij zijn onregelmatig vertakt, terwijl de polypen langgesteeld zijn; de steeltjes hebben eveneens een gegolfd periderm zonder duidelijke ringen. De meeste hydranthen van deze laatste kolonies zijn sterk gecontraheerd.

Bougainvillia ramosa komt in groote hoeveelheden in de haven van Den Helder voor, voornamelijk in den typischen vorm (forma *typica* Brink, 1925). Exemplaren welke tot de forma *benedeni* gebracht moeten worden, komen hoofdzakelijk voor op plaatsen met een aanmerkelijke waterbeweging, die van veel invloed schijnt te zijn op de vorming van schizosporen (cf. Brink, 1925). Ook andere oecologische factoren hebben veel invloed op den vorm en den bouw van deze zeer variable soort (cf. Hallez, 1905; Brink, 1925). In het Zuiderzeegebied is zij aangetroffen bij Enkhuizen (Enkhuizerzand) en ten zuiden van de Javaruggen; op beide plaatsen werd zij vóór 1932 verzameld. Hoewel Funke (1922) de exemplaren van de Javaruggen als *Bougainvillia flavida* Hartlaub, 1897, vermeldt, behooren zij met groote zekerheid tot *B. ramosa*; de twijfelachtige *B. flavida* is slechts éénmaal (door

HARTLAUB) bij Helgoland aangetroffen. De door FUNKE (loc. cit.) als *Bougainvillia ramosa* vermelde en afgebeelde exemplaren behooren tot *Cordylophora caspia* (Pall., 1771). Ook in de kustwateren is *B. ramosa* aangetroffen, nl. bij Vlieland en bij de Terschellingerbank (cf. LELOUP, 1933).

Cuspidella costata Hincks, 1868

Kornwerderzand, 30 Sept. 1938, no. 393. Enkele ledige hydrothecae op den hydrocaulus van *Bougainvillia ramosa* (Wright).

Hoewel van deze soort zeer weinig materiaal aanwezig is, komt de vorm der hydrothecae goed met de door HUMMELINCK (1936, fig. 4) gegeven afbeeldingen overeen. De determinatie van het Zuiderzee-materiaal wordt door HUMMELINCK (loc. cit.) als eenigszins twijfelachtig beschouwd, daar Europeesch materiaal van *C. costata* slecht bekend is. Door RITCHIE (1910) is materiaal van deze soort uit Achter-Indië iets uitvoeriger besproken, terwijl de door STECHOW (1923) als *Cuspidella gigantea* beschreven polypen uit de Sagami Baai zeer waarschijnlijk met het door RITCHIE beschreven materiaal identiek zijn. Het Zuiderzee- en Waddenzee-materiaal komt met de beschrijving van RITCHIE goed overeen, zoodat met vrij groote zekerheid zoowel de exemplaren van RITCHIE en STECHOW als het bovenvermelde Zuiderzee- en Waddenzee-materiaal tot een zelfde soort gebracht moeten worden. Het verspreidingsgebied van *C. costata* is waarschijnlijk zeer groot, evenals dit voor *Laomedea bicuspidata* Clark, 1875, het geval is. De hydrothecae van het Waddenzee-materiaal van *C. costata* zijn leeg en bevatten geen spoor meer van de hydranthen. In Nederland is *Cuspidella costata* alleen nog aangetroffen in den mond van de voormalige Zuiderzee, nl. bij den Breehorn, ten noorden van Wieringen, op een hydrocaulus van *Laomedea* en op een stukje vuursteen.

Campanulina cf. *lacerata* (Johnston, 1847)

Vliestroom, 25 Aug. 1938, no. 205. Enkele kolonies met kruipende hydrorhiza tusschen *Laomedea dichotoma* (L.) op *Balanus*. Geen gonothecae.

De kolonies van den Vliestroom, welke voorloopig bij *Campanulina lacerata* zijn ondergebracht, bestaan uit een aantal kruipende hydrorhizabuizen, waarvan zich de afzonderlijke hydrothecae verheffen, terwijl zich soms een hydrocaulus ontwikkelt, die maximaal een hoogte van 7 mm bereikt. *C. lacerata* heeft doorgaans kolonies met een duidelijk ontwikkelden hydrocaulus, de hydro- en gonothecae bevinden zich aan de vertakkingen hiervan of dadelijk aan den hydrocaulus. Door verschillende auteurs worden kruipende kolonies van deze soort vermeld (cf. KRAMP, 1932); bij deze kolonies verheffen zich hydro- en gonothecae dadelijk van de hydrorhiza. Dergelijke kolonies kunnen alleen bij aanwezigheid van de gonothecae van *C. pumila* (Clark) (CLARK, 1875) (= *C. nana* Hartlaub, 1897) onderscheiden worden. Door HUMMELINCK (1936) worden kolonies van *C. pumila* beschreven met een gering ontwikkelden hydrocaulus. De vrouwelijke gonothecae van *C. pumila* hebben een korten, buisvormigen kraag aan het distale gedeelte, deze kraag ontbreekt bij de vrouwelijke gonotheca van *C. lacerata*, welke afgeknot is. De verschillen zijn echter gering en de mogelijkheid is niet uitgesloten dat beide typen van gonothecae vroeger of later aan de zelfde kolonie worden aangetroffen, in welk geval *C. pumila* een synonym van *C. lacerata* zou worden. Steriele kolonies van beide „soorten" kunnen niet met zekerheid onderscheiden worden.

C. lacerata komt in groote aantallen voor in de haven van Den Helder; in het voormalige Zuiderzeegebied was zij vóór 1932 een der meest algemeene soorten (cf. HUMMELINCK, 1936). Zij werd ook op verscheidene plaatsen ten noorden van Wieringen aangetroffen, waar de soort de afsluiting in 1932 heeft overleefd. *C. pumila* is tot nu toe in het Zuiderzeegebied alleen ten noorden van Wieringen gevonden (Breehorn), te zamen met *Cuspidella costata* en *Laomedea* op een stukje vuursteen; ook deze soort heeft mogelijk de afsluiting overleefd.

Calicella syringa (Linnaeus, 1758)

Oostmeep, 29 Aug. 1938. Een groot aantal hydrothecae op den hydrocaulus van *Laomedea* en op de hydranthensteeltjes en gonothecae van *Campanularia johnstoni* Ald. Geen gonothecae aanwezig.

Schuitengat, 30 Aug. 1938. Vele hydrothecae op *Sertularia cupressina* L. Geen gonothecae aanwezig.

De hydranthen van de kolonies van *Calicella syringa* zijn nog in goeden staat in de hydrothecae te zien, zoodat deze soort ongetwijfeld levend werd verzameld. De steeltjes der hydrothecae hebben ongeveer 3/4 van de lengte der thecae en zijn over de geheele lengte spiraalvormig gewonden. De hydrothecae zijn vrij klein, zij schommelen in lengte tusschen 375 en 425 μ terwijl zij een diameter van ± 120 μ hebben.

Calicella syringa is een zeer gewone soort in de haven van Den

Helder, waar zij in groot aantal op *Laomedea*, *Sertularia* en *Hydrallmania* wordt aangetroffen, terwijl zij zoo nu en dan ook op algen wordt gevonden. In het voormalige Zuiderzeegebied werd zij slechts tweemaal aangetroffen; beide vindplaatsen liggen ten noorden van den afsluitdijk, nl. in het Amsteldiep op *Sertularia cupressina* en in den Breehorn, te zamen met *Cuspidella costata*, *Campanulina lacerata* en *Laomedea*, op een stukje vuursteen. Op beide plaatsen is de soort mogelijk nog aan te treffen. *Calicella syringa* wordt zoo nu en dan ook aangespoeld op andere Hydroiden en op algen langs het Nederlandsche Noordzeestrand aangetroffen.

Sertularia cupressina Linnaeus, 1758

Vliestroom, 25 Aug. 1938, no. 206. Een kleine, ± 10 mm hooge kolonie op een stukje steen. Hydrothecae met goed behouden hydranthen. Enkele jonge gonothecae aanwezig.

Oostmeep, 29 Aug. 1938. Brokstukken van een flinke kolonie te zamen met *Laomedea longissima* (Pall.) en vele algen. Hydrothecae met goed bewaarde hydranthen.

Schuitengat, 30 Aug. 1938. Vele goed ontwikkelde kolonies en talrijke brokstukken met vele gonothecae. De hydrothecae hebben duidelijke gecontraheerde hydranthen. Sommige hydrocauli met *Calicella syringa* (L.).

Het is bekend dat *Sertularia cupressina* in flinke hoeveelheden in den mond van de Zuiderzee en op verschillende plekken in de Waddenzee voorkwam (cf. REDEKE, 1909; FUNKE, 1917). Op sommige plaatsen kwam zij zelfs zoo overvloedig voor, dat zij daar gevischt werd door visschers van Texel, Wieringen, Terschelling en een aantal kleine dorpen langs de Friesche kust. Voor velen van deze visschers was het gedroogde product een belangrijke bron van inkomsten. Deze visscherij op „weerboompjes", zooals *S. cupressina* en verwante soorten (bv. *Hydrallmania falcata* (Linnaeus, 1758)) door de Nederlandsche visschers gewoonlijk genoemd werden, is nu vrijwel geheel verdwenen en de uitgestrektheid van de „zeemosvelden" is sterk teruggeloopen. In hoeverre deze vermindering het gevolg is van de vroeger zeer intensieve visscherij is niet bekend. Zeemosvelden van eenige uitgestrektheid werden aangetroffen bij de Oostmeep, Noordmeep, Blauwe Slenk en in den mond van de Zuiderzee (ten noorden van het vroegere eiland Wieringen en bij het Kornwerderzand). Deze zeemosvelden bestonden voornamelijk uit *S. cupressina* f. *typica* Broch en *S. cupressina* f. *argentea* L. *Hydrallmania falcata* (L.), die langs de Duitsche waddenkust zoo veelvuldig voorkwam dat zij daar velden van flinke uitgestrektheid vormde, wordt bij ons nooit in zulke hoeveelheden gevonden, maar treedt tusschen *Sertularia cupressina* geregeld op. In de Waddenzee-verzameling ontbreekt deze laatste soort geheel; zij is echter gevonden in de haven van Den Helder en ten noorden van Wieringen, nl. in het Amsteldiep. Op één vindplaats in de Waddenzee (Schuitengat) werd in 1938 *Sertularia cupressina* in zulke hoeveelheden opgehaald dat aangenomen mag worden dat het net een zeemosveld passeerde.

Campanularia johnstoni Alder, 1856

Oostmeep, 26 Aug. 1938. Talrijke kolonies met *Calicella syringa* (L.) op hydrocauli van *Laomedea*. Rijpe gonothecae aanwezig.

Schuitengat, 30 Aug. 1938. Een groot aantal hydro- en gonothecae die zich verheffen van een kruipende hydrorhiza op *Codium* en *Alcyonidium*.

Kornwerderzand, 30 Sept. 1938, no. 393. Talrijke kruipende kolonies op *Ceramium* en *Fucus*, te zamen met *Laomedea dichotoma* (L.) en *Bougainvillia ramosa* (Wright). Rijpe en ledige gonothecae aanwezig.

De kolonies van *Campanularia johnstoni* welke in de verzameling aanwezig zijn, vallen in twee typen uiteen. Bij het eerste type, dat vertegenwoordigd wordt door de kolonies van het Kornwerderzand, zijn de hydrothecae iets cylindrisch en over het algemeen kleiner dan bij die van het tweede type, waar de hydrothecae meer komvormig zijn. De lengte van de hydrothecae van het eerste type varieert tusschen 525 en 675 μ, de diameter tusschen 300 en 375 μ. De rand van de theca heeft duidelijke kanteelvormige tanden, de steel van de theca is 2 à 4 maal zoo lang als deze. Deze steel heeft aan onder- en bovenzijde duidelijke ringen, terwijl het periderm van het stuk tusschen deze ringen gegolfd is; zij zijn nooit vertakt, zoodat alle hydrothecae en gonothecae dadelijk van de hydrorhiza ontspringen. De kolonies van het tweede type, vertegenwoordigd door de kolonies van de Oostmeep en het Schuitengat, hebben grootere, meer komvormige hydrothecae, varieerend in lengte tusschen 700 en 750 μ, met een diameter van ± 450 μ. De tanden langs den rand zijn meer afgerond dan bij die van het eerste type, hoewel het aantal vrijwel hetzelfde is (8 tot 12). De steeltjes der hydrothecae zijn lang en kunnen een lengte van 8 mm bereiken, zij zijn dikwijls vertakt of dragen gonothecae. Aan de basis van den steel en vlak onder de theca bevinden zich enkele duidelijke ringen, het periderm van het deel tusschen deze ringen is glad of flauw gegolfd. De gonothecae van beide typen toonen geen verschillen. Ongetwijfeld behooren beide vormen tot één zelfde soort, nl. *Campanularia* *johnstoni*. Kolonies van het tweede type worden in enorme hoeveelheden op allerlei drijvende of vaste voorwerpen in het Noordzeegebied gevonden en spoelen gedurende het geheele jaar in groot aantal langs het geheele Nederlandsche Noordzeestrand aan. Zij vertegenwoordigen waarschijnlijk het type, dat gewoonlijk onder zuiver mariene condities leeft. Kolonies van het eerste type treden waarschijnlijk op plaatsen met een iets verlaagd zoutgehalte op. De door FUNKE (1922) vermelde *Campanularia volubilis* (Linnaeus, 1758) van den mond van de Zuiderzee (ten zuiden van de Javaruggen) behoort zeer waarschijnlijk tot het eerste type. BROCH (1933) heeft uitvoerig de variabiliteit van *C. johnstoni* besproken; de aanmerkelijke variatie waaraan deze soort onderhevig is, blijkt ook duidelijk als exemplaren van verschillende Nederlandsche vindplaatsen vergeleken worden. *C. johnstoni* komt in groote aantallen in de haven van Den Helder voor, in het voormalige Zuiderzeegebied werd zij ten noorden van Wieringen aangetroffen, nl. in het Amsteldiep en in het Gaatje, waar de soort mogelijk nog levend voorkomt.

Laomedea longissima (Pallas, 1766)

Oostmeep, 26 Aug. 1938. Een 6 cm lange hydrocaulus met enkele verspreide hydrothecae. Geen gonothecae.

Slenk, 29 Aug. 1938. Een groot aantal hydrocauli met zeer donker gekleurd periderm. Geen hydro- of gonothecae.

Oostmeep, 29 Aug. 1938. Een 7 cm lange hydrocaulus met enkele hydrothecae.

Schuitengat, 30 Aug. 1938. Verschillende donkergekleurde hydrocauli zonder hydro- en gonothecae, welke waarschijnlijk tot deze soort behooren.

Kornwerderzand, 29 Sept. 1938, no. 372. Een kolonie van 7.5 cm hoogte op *Cardium*. Zeer veel hydro- en gonothecae aanwezig.

Laomedea longissima is in de Waddenzee-collectie niet overvloedig vertegenwoordigd. De kolonies van de Oostmeep en het Kornwerderzand zijn in goede conditie, de rest van het materiaal van deze soort bestaat uit doode hydrocauli met zeer donker gekleurd periderm. *L. longissima* kan niet altijd gemakkelijk van *L. dichotoma* (L.) onderscheiden worden, kolonies van middelmatige grootte geven vaak groote moeilijkheden (zie onder *L. dichotoma*). Beide soorten komen veelvuldig in de haven van Den Helder voor, maar *L. longissima* is daar veel talrijker dan *L. dichotoma*. *L. longissima* werd ook op verschillende plaatsen in den mond van de Zuiderzee aangetroffen voor deze in 1932 werd afgesloten. In den Breehorn ten noorden van Wieringen, waar zij eveneens is gevonden, kan de soort waarschijnlijk nog steeds levend gevonden worden, daar zij langs den noordkant van Wieringen nog geregeld wordt aangetroffen; in de collectie van het Rijksmuseum van Natuurlijke Historie te Leiden bevinden zich bovendien exemplaren van deze soort welke op de wadden aan den oostkant van Texel en Vlieland en langs de noordkust van Friesland en Groningen zijn verzameld. De soort is ongetwijfeld zeer talrijk in de wateren voor de Nederlandsche kust; gedurende het geheele jaar spoelt zij langs het Noordzeestrand in flinke aantallen aan. Na stormen kunnen de donkergekleurde hydrocauli zelfs een groot stuk van het strand bedekken. Waarschijnlijk worden de stevige kolonies door de waterbewegingen over aanmerkelijke afstanden getransporteerd, terwijl het ook niet uitgesloten is, dat zij door de sterke stroomingen in de zeegaten tusschen de Waddeneilanden uit de Noordzee in de Waddenzee gebracht worden. De aanwezigheid van hydrocauli van deze soort in het Schuitengat en bij de Slenk beteekent daarom niet dat de soort daar ook levend wordt aangetroffen.

Laomedea dichotoma (Linnaeus, 1758)

Blauwe Slenk, 30 Aug. 1937. Talrijke kolonies met *Balanus* op steenen, 8–45 mm hoog. Veel gonothecae aanwezig.

Vliestroom, 25 Aug. 1938, no. 205. Vele kolonies met gonothecae op *Balanus* en op stukjes steen, in hoogte varieerend tusschen 3 en 15 mm, te zamen met *Campanulina* cf. *lacerata* (Johnst.), *Membranipora* en *Alcyonidium*.

Vliestroom, 25 Aug. 1938, no. 206. Een groot aantal kleine, 2–8 mm hooge kolonies op *Balanus* en stukjes steen, te zamen met *Membranipora* en *Farrella*. Geen gonothecae.

Westmeep, 26 Aug. 1938, no. 247. Talrijke kolonies op steenen, schelpen en op *Balanus*, met *Membranipora* en *Alcyonidium*. Hoogte tot 7 mm, geen gonothecae.

Westmeep, 26 Aug. 1938, no. 249. Talrijke kolonies op steenen en op *Balanus*, te zamen met *Laomedea neglecta* Ald. en *Membranipora*. Hoogte tot 12 mm, veel gonothecae aanwezig.

Slenk, 29 Aug. 1938. Zeer veel kolonies op algen, tot 15 mm hoog. Geen gonothecae.

Schuitengat, 30 Aug. 1938. Verschillende kleine, tot 8 mm hooge kolonies op *Ulva*. Talrijke gonothecae in verschillende ontwikkelingsstadia aanwezig.

Kornwerderzand, 29 Sept. 1938, no. 372. Talrijke kolonies op *Balanus* en *Mytilus*, in hoogte varieerend tusschen 15 en 80 mm. Veel gonothecae aanwezig.

Kornwerderzand, 29 Sept. 1938, no. 373, Talrijke tot 60 mm hooge kolonies op *Mytilus*, *Mya* en *Balanus*. Talrijke rijpe gonothecae aanwezig.

Kornwerderzand, 30 Sept. 1938, no. 393. Verschillende 10–15 mm hooge kolonies met *Bougainvillia ramosa* (Wright) en *Campanularia johnstoni* Ald. op *Ceramium*. Zeer veel rijpe en ledige gonothecae aanwezig.

Laomedea dichotoma is door een groot aantal kolonies in de Waddenzeecollectie vertegenwoordigd, zoodat aangenomen kan worden dat de soort in dit gebied zeer talrijk en over het geheele gebied verspreid voorkomt. De kolonies bereiken soms een aanmerkelijke hoogte (tot minstens 80 mm); het is niet eenvoudig zulke flink ontwikkelde kolonies van die van *L. longissima* te onderscheiden. Alle kolonies van *L. dichotoma* bestaan uit een duidelijken, monosiphonen hydrocaulus, welke zich van een kruipende hydrorhiza verheft. Deze hydrorhiza heeft een stevig periderm en heeft ongeveer denzelfden diameter als de hydrocaulus aan de basis. Het periderm van den hydrocaulus is eveneens sterk ontwikkeld, de kleur van dit periderm varieert tusschen geel en vrij donker geelbruin. De kolonies met een donker gekleurden hydrocaulus vertoonen zeer veel gelijkenis met *L. longissima* en kunnen alleen door middel van den vorm der hydrothecae onderscheiden worden. De bouw van de kolonie is bij *L. dichotoma* aan aanmerkelijke variatie onderhevig. Bij de jonge kolonies is de hydrocaulus nog duidelijk en zijn de zijtakken kort, in oudere kolonies echter kunnen de onderste zijtakken even lang als de hoofdstam worden en kunnen zij dezelfde kleur vertoonen, zoodat de hydrocaulus dan veel minder opvalt. Bij *L. longissima* draagt de hydrocaulus in den regel korte zijtakken, terwijl de kleur van het periderm van den hoofdstam en de voornaamste vertakkingen donker bruinzwart is. Kolonies van *L. longissima* die het „*dichotoma*" type dicht benaderen worden echter ook aangetroffen. De hydrothecae van *L. dichotoma* zijn geplaatst op steeltjes van wisselende lengte; deze steeltjes zijn gewoonlijk over hun geheele lengte geringd (het aantal ringen bedraagt dan 5 tot 25), maar zoo nu en dan worden ook hydrothecae op steeltjes gevonden, die alleen basaal en terminaal geringd zijn, terwijl het stuk tusschen de ringen glad is. De hydrothecae zijn bekervormig soms met iets cylindrische wanden, 360-420 μ lang, ± 250 μ breed en zeer teer, zoodat het niet gemakkelijk is den rand duidelijk te zien. Er zijn ongeveer 10 à 12 marginale tanden, welke zeer laag en stomp zijn. Op dwarse doorsnede even beneden den rand blijkt de hydrotheca veelhoekig te zijn. Bij *L. longissima*, waar de hydrothecae iets grooter zijn, is de dwarse doorsnede even onder den rand zuiver cirkelrond of zeer weinig gegolfd. De ontwikkeling van de marginale tanden varieert bij deze laatste soort aanzienlijk. Gewoonlijk zijn er 14-18 duidelijke, stompe tanden, gescheiden door halfcirkelvormige insnijdingen, maar zoo nu en dan worden ook hydrothecae met een vrijwel gladden of iets gegolfden rand aangetroffen. De basale kamer van de hydrotheca van *L. dichotoma* is altijd symmetrisch; bij *L. longissima* is deze gewoonlijk symmetrisch, terwijl hydrothecae met een asymmetrische basale kamer niet zeldzaam zijn. Er zijn geen verschillen tusschen de gonothecae van beide soorten, die gewoonlijk op geringde steeltjes zijn geplaatst. Bij *L. longissima* worden zij gevonden in den oksel van de steeltjes der hydrothecae; bij *L. dichotoma* worden de gonothecae ook op de steeltjes der hydrothecae dicht onder de theca aangetroffen. Beide soorten produceeren vrije medusen van het *Obelia* type. Dergelijke medusen worden ook voortgebracht door *Laomedea geniculata* (L.) en misschien ook door *Laomedea bicuspidata* (Clark). De volwassen medusen van deze vier soorten zijn slecht bekend, maar het is niet onwaarschijnlijk dat de volwassen meduse van *L. longissima* van de overige *Obelia* medusen verschilt en als *Obelia nigra* Browne, 1900, onderscheiden kan worden (cf. KRAMP, 1939). Het eenige betrouwbare kenmerk om de kolonies van *L. dichotoma* en *L. longissima* te onderscheiden is de vorm van den rand der hydrotheca.

Laomedea dichotoma komt in gering aantal in de haven van Den Helder voor; evenals *L. longissima* werd zij op verschillende plaatsen in den mond van de voormalige Zuiderzee aangetroffen. Zij is ook ten noorden van Wieringen verzameld, waar de soort mogelijk de afsluiting van de Zuiderzee in 1932 heeft overleefd. In de Waddenzee blijkt het de meest voorkomende hydropolyp te zijn.

Laomedea geniculata (Linnaeus, 1758)

Schuitengat, 30 Aug. 1938. Een groot aantal tot 8 mm hooge kolonies op *Fucus* en *Laminaria*. Enkele gonothecae aanwezig.

De ontwikkeling van de peridermverdikking onder den polypensteel en van den abcaulinen wand van de theca, is bij *L. geniculata* aan schommelingen onderhevig. De kolonies op *Laminaria* en enkele kolonies op *Fucus* bezitten de karakteristieke, stevige peridermverdikking, zij zijn onvertakt, de zig-zagsgewijze gebogen hydrocaulus draagt een hydrotheca op iederen knik. De overige kolonies op *Fucus* hebben een nauwelijks zichtbare peridermverdikking en zijn bovendien vertakt. Wanneer materiaal van *L. geniculata* van verschillende vindplaatsen wordt vergeleken, worden echter alle mogelijke overgangen tusschen beide typen aangetroffen. De soort is zeer talrijk op *Fucus*, *Laminaria* en andere algen in de haven van Den Helder. Zij werd echter nooit in de Zuiderzee aangetroffen, hetgeen voor deze duidelijk euryhaliene soort zeer opmerkelijk genoemd moet worden. In de collectie van het Zoölogisch Station bevinden zich goed ontwikkelde kolonies uit het Amelander Gat. *L. geniculata* komt naar alle waarschijnlijkheid in de Nederlandsche kustwateren zeer talrijk voor, daar zij gedurende het geheele jaar aangespoeld op het strand wordt aangetroffen.

Laomedea neglecta Alder, 1856

Westmeep, 26 Aug. 1938, no. 249. Een aantal kleine, 3–5 mm hooge kolonies op steenen en op *Balanus*, tezamen met *Laomedea gelatinosa* (Pall.) en *Laomedea dichotoma* (L.). Geen gonothecae aanwezig.

Kornwerderzand, 29 Sept. 1938, no. 372. Verschillende kleine, ± 5 mm hooge kolonies op den hydrocaulus van *Laomedea dichotoma* (L.) op *Balanus* en *Mytilus*. Geen gonothecae aanwezig.

Kornwerderzand, 29 Sept. 1938, no. 373. Enkele kolonies van 2 tot 10 mm hoogte met *Laomedea dichotoma* (L.) op *Balanus* en op *Mytilus*. Geen gonothecae aanwezig.

Van *Laomedea neglecta* zijn alleen steriele kolonies in de Waddenzee-collectie aanwezig. Kolonies met rijpe gonothecae zijn maar eenmaal in het Nederlandsche gebied verzameld, nl. in den Breehorn ten noorden van Wieringen, waar de soort mogelijk na de afsluiting is blijven leven. Steriele exemplaren, welke met groote waarschijnlijkheid eveneens tot *L. neglecta* gebracht dienen te worden, zijn vóór de afsluiting gevonden in den mond van de Zuiderzee, nl. bij Kreupel, Gammels en Vrouwenzand, en in de haven van Den Helder (cf. HUMMELINCK, 1930, 1936). Het is echter niet mogelijk de steriele kolonie met voldoende zekerheid van jonge exemplaren van *Laomedea gelatinosa* (Pall.) te onderscheiden, welke laatste soort zeer talrijk was in de voormalige Zuiderzee en ook in de haven van Den Helder in groote hoeveelheden werd aangetroffen. Hoewel de kolonies uit de Waddenzee met fertiele exemplaren van *L. neglecta* zeer goed overeenkomen, moet de determinatie toch met eenig voorbehoud worden beschouwd. Alle kolonies hebben een monosiphonen hydrocaulus, welke zich van een kruipende hydrorhiza verheft. Enkele van de wat meer ontwikkelde hydrocauli van het Kornwerderzand vertoonen aan hun basis eenige secundaire buizen, die den eersten zijtak bereiken. De vertakking van de kolonies is zeer onregelmatig; de hydrothecae zijn geplaatst aan vrij lange steeltjes, die bestaan uit geringde en gladde stukken. Dadelijk onder elke theca bevindt zich een geringd stuk bestaande uit 3 tot 5 ringen. De hydrothecae zijn zeer slank en teer, zij varieeren in lengte tusschen 300 en 390 μ, met een diameter van 120 tot 150 μ. De wanden van de theca zijn vrijwel cylindrisch en de basale kamer is iets asymmetrisch tengevolge van de scheeve plaatsing van het diaphragma. De rand heeft 8-10 dubbele tanden, die door halfcirkelvormige insnijdingen zijn gescheiden; iedere tand heeft een afgeronde apicale insnijding, zoodat de hoek van iederen tand tot een klein tandje vervormd is; deze insnijding is echter veel minder diep dan die welke de dubbele tanden scheidt. Op dwarse doorsnede even onder den rand blijkt de theca duidelijk gegolfd te zijn.

Laomedea gelatinosa (Pallas, 1766)

Westmeep, 26 Aug. 1938, no. 249. Een kleine kolonie van 6 mm hoogte met *Laomedea dichotoma* (L.) op *Balanus*. Geen gonothecae aanwezig.

De exemplaren van *L. gelatinosa* in de Waddenzee-verzameling verschillen van die van *L. neglecta* door de veel grootere hydrothecae, die meer komvormig zijn en minder cylindrische wanden bezitten; de bouw der tanden komt echter bij beide soorten vrijwel overeen. Het diaphragma van de hydrothecae van *L. gelatinosa* is duidelijk, de basale kamer is symmetrisch. De steriele kolonies van *L. gelatinosa* van de Westmeep komen goed met fertiele exemplaren overeen. De soort is zeer talrijk in de haven van Den Helder, terwijl zij in de geheele voormalige Zuiderzee zeer talrijk voorkwam (cf. HUMMELINCK, 1936).

Laomedea spec.

Vleistroom, 25 Aug. 1938, no. 207. Verschillende ± 10 mm hooge hydrocauli.

Op de bovengenoemde vindplaats werden een aantal doode hydrocauli zonder hydro- en gonothecae verzameld, welke niet met voldoende zekerheid gedetermineerd kunnen worden.

Wat betreft de vertikale en horizontale verspreiding der in de Waddenzee aangetroffen soorten kan het volgende worden opgemerkt. Alle in aanmerking komende soorten behooren tot het litorale gebied, m.a.w. zij worden hoofdzakelijk in de bovenste waterlagen aangetroffen. De grootste diepte waaruit in de Waddenzee Hydroiden werden opgehaald bedraagt 27 m. *Laomedea geniculata* behoort tot de getijdezone; het voorkomen van deze soort in de getijdezone zal, evenals dit voor de in de Waddenzee-verzameling niet aanwezige *Laomedea flexuosa* Alder, 1850, het geval zal zijn, hoofdzakelijk worden bepaald door het voorkomen van groote bruinwieren in deze zone. *L. geniculata* dringt ten gevolge van het geregelde voorkomen op *Laminaria* ook dieper gelegen gebieden binnen. De overige in de Waddenzee-verzameling aangetroffen soorten komen slechts sporadisch in de getijdezone voor, gewoonlijk bewonen zij dieper gelegen wateren; alleen *Campanularia johnstoni* en *Tubularia larynx* komen zoo nu en dan in groote aantallen in de getijdezone voor, zonder evenwel een geregeld bestanddeel hiervan te vormen. Broch (1928) heeft er reeds eerder op gewezen dat de meeste hydropolypen als duidelijk eurybaath moeten worden beschouwd, zoodat het lastig is bepaalde soorten als karakteristieke representanten van een bepaalde, meer of minder scherp begrensde zone op te vatten.

Nog moeilijker en vaak zelfs geheel ondoenlijk is het de hydropolypen over de verschillende geographische gebieden te verdeelen of hen te beschouwen als karakteristieke bestanddeelen van bepaalde faunagebieden. Het verspreidingsgebied van de meeste goed bekende soorten is zeer groot ten gevolge van hun duidelijke eurythermie. Deze heeft tot gevolg dat vele soorten, welke als planula door de zeestroomingen op ver afgelegen, meer of minder ongunstige plaatsen worden gedeponeerd, wel kolonies ontwikkelen, maar zich niet verder voortplanten. Daar gewoonlijk opgaven over de ontwikkeling der gonophoren of de conditie waarin de kolonie werd aangetroffen ontbreken, is het zelfs voor de meest algemeene soorten practisch onmogelijk het gebied te reconstrueeren, waarbinnen zij zich geregeld voortplanten en dat dus als hun woongebied in strikteren zin moet worden beschouwd. Zelfs voor een beperkt gebied als Nederland is over de periode van geslachtsrijpheid der gonophoren en het al of niet periodiek optreden van polypen- en (of) medusengeneratie der weinige inheemsche soorten zoo goed als niets bekend.

Vrijwel alle in de Waddenzee aangetroffen soorten hebben hun voornaamste verspreiding in boreale gebieden; zij zijn dientengevolge in de Noordzee talrijk (*Tubularia larynx*, *Bougainvillia ramosa*, *Campanulina lacerata*, *Calicella syringa*, *Sertularia cupressina*, *Campanularia johnstoni*, *Laomedea dichotoma*, *Laomedea geniculata*, *Laomedea gelatinosa*). Het voorkomen van deze soorten is echter geenszins tot het boreale gebied beperkt. *Laomedea geniculata* en *L. longissima* zijn cosmopolieten, die alleen onder zuiver arctische condities minder talrijk voorkomen; *Tubularia larynx*, *Bougainvillia ramosa*, *Campanularia johnstoni* en *Laomedea gelatinosa* zijn ook in het mediterraan-atlantische gebied zeer talrijk. *Laomedea dichotoma* komt wat zijn verspreiding betreft in groote trekken met *L. longissima* overeen, is echter minder cosmopoliet, terwijl het verspreidingsgebied van *Cuspidella costata* en *Laomedea neglecta* slecht bekend is. De hydropolypen-bevolking van de Waddenzee, evenals die van de vroegere Zuiderzee draagt een overwegend boreaal karakter en bestaat uit Noordzee-soorten. De sporadische vermelding van *Cuspidella costata* in de Noordzee is waarschijnlijk een gevolg van de geringe afmetingen van de polyp, waardoor deze makkelijk over het hoofd gezien wordt; het voorkomen van *Laomedea neglecta* in de Waddenzee is twijfelachtig, terwijl deze soort in de Noordzee eerst in den laatsten tijd is aangetroffen, mogelijk een gevolg van verwarring met *Laomedea gelatinosa*. In de volgende tabel is de verspreiding van de in de Waddenzee aangetroffen soorten weergegeven.

— in het gebied nog niet aangetroffen ? misschien in het gebied gevonden r in het gebied zeldzaam × in het gebied algemeen	Waddenzee	Mond van de Zuiderzee ten N. van den afsluitdijk	Zuiderzee ten Z. van den afsluitdijk, vóór 1932	Haven van Den Helder	Noordzeegebied
Tubularia larynx	?	r	—	×	×
Bougainvillia ramosa	r	r	r	×	×
Cuspidella costata	—	r	—	—	r
Campanulina lacerata	?	—	×	×	×
Calicella syringa	×	×	—	×	×
Sertularia cupressina	×	×	?	r	×
Campanularia johnstoni	×	×	r	×	×
Laomedea longissima	×	×	r	×	×
Laomedea dichotoma	×	×	r	r	×
Laomedea geniculata	×	r	—	×	×
Laomedea neglecta	?	?	r	—	r
Laomedea gelatinosa	r	×	×	×	×

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THE DEVELOPMENT OF THE EGG OF LIMNAEA STAGNALIS L. FROM THE FIRST CLEAVAGE TILL THE TROCHOPHORE STAGE, WITH SPECIAL REFERENCE TO ITS "CHEMICAL EMBRYOLOGY"

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In a previous paper (RAVEN 1945), I have treated the development of the egg of *Limnaea stagnalis* from oviposition till first cleavage. Beside the morphological processes during this period, also the physical changes had been studied; moreover, the chemical composition of the egg had been investigated with the aid of cytochemical methods.

In the present paper, this study is continued with regard to the subsequent phases of development, beginning with the 1st cleavage division and ending at the trochophore stage. No special attention has been paid to the purely morphological phenomena of development (e.g. cell lineage), which have been studied in a quite satisfactory manner by previous authors. However, the histological differentiation of the cells has been followed with much accuracy; moreover, the chemical changes accompanying development have been pursued using a variety of cytochemical methods. Thus, the present paper forms a contribution to the "chemical embryology" of *Limnaea.*

MATERIAL AND METHODS

Egg-masses were obtained in the manner described in a previous paper (RAVEN & BRETSCHNEIDER 1942). Their development was studied by a variety of methods. The eggs were studied in the living state, both untreated and after vital staining with neutralred, nile blue hydrochloride, brilliant cresyl violet, cresylechtviolet, methylene blue, Janusgreen, trypan blue, and indigocarmine. Whole eggs were delivered from their capsules and subjected to the following cytochemical reactions (cf. LISON 1936 for technical details): benzidine peroxidase reaction; M-nadi oxidase reaction for the detection of indophenol blue oxidase; rongalite white for leucomethylene blue oxidoreducase. The localization of sulfhydril compounds was studied by the reaction with alkaline sodium nitroprussiate, that of glycogen with the iodine reaction and of fat by staining with Scharlach.

Furthermore, great numbers of eggs in all stages of development were fixed in the fluids of BOUIN, ZENKER, CARNOY and CHAMPY, in alcohol, formol, trichloracetic acid and sublimate-acetic. The fixed eggs were enclosed in agar, then dehydrated and embedded in paraffine. Sections mostly $7\frac{1}{2}$ μ.

In total, 382 sectioned eggs have been studied. The greatest number (154) has been fixed in BOUIN and stained with iron haematoxylin and eosin or with azan; the remaining eggs served for the study of special cell components: Golgi bodies (osmic acid), mitochondria (after BENDA, ALTMANN and with iron haematoxylin), fat (osmic acid), glycogen (methods of BEST and of BAUER), thymonucleic acid (FEULGEN-reaction), ribonucleic acid (after BRACHET 1942), sulfhydril compounds (after CHÈVREMONT & FRÉDÉRIC 1943). In this way, a general survey of the localization of cell substances in the successive stages of development has been obtained.

DESCRIPTIVE PART

I. From the first cleavage till the 8-cell stage

1. External appearance. Fig. 1 shows a number of microphotographs, taken at various moments during the first 3 cleavages of the egg. They represent characteristic phases of the cleavage process and will serve us as landmarks for a subdivision of this process. The times indicated are average times of development at 20°C., computed from a great number of eggs. The total duration of the period, from the stage of fig. 1^1 to that of fig. 1^{19}, is about 235 minutes.

After a preliminary elongation of the egg, perpendicular to the egg axis, the cleavage furrow appears as an indentation at the animal pole (fig. 1^1). It extends around the egg and after 4 minutes it reaches the vegetative pole (fig. 1^2). Then, the furrow deepens from all sides, the animal side, however, remaining ahead. 13 Minutes after the first indication of the cleavage furrow, it has entirely cut through the egg, the two blastomeres remaining in contact by a very narrow stalk only (fig. 1^4). At this moment, the furrow has got its greatest depth; the blastomeres, which are equal in size, have become nearly spherical. Now, the reverse process sets in, the blastomeres gradually flattening against each other (fig. 1⁵⁻⁷). At 56 minutes, this flattening is completed; the cleavage furrow is now hardly visible, in its place a cell wall bounds the two blastomeres (fig. 1⁷). At the same time, the first indications of the cleavage cavity become visible as small transparent spots in the region of this cell wall. Soon, they fuse into a single lenticular cavity between the blastomeres (fig. 1⁸). This cavity widens progressively (fig. 1⁹), and may attain such dimensions that the two blastomeres appear in optical section like narrow crescents surrounding a nearly circular cavity. In many eggs, however, before this stage is reached, the cleavage cavity breaks through to the exterior and its contents flow out, as has been described extensively by COMANDON & DE FONBRUNE (1935); the egg shrinks to the shape of fig. 1⁷ or 1⁸. This expulsion of fluid may be repeated a second time before the beginning of the 2d cleavage; on the other hand, in many eggs the cleavage cavity remains intact till shortly before the stage of fig. 1¹¹. The moment at which the cleavage cavity breaks through seems to be, therefore, rather fortuitous.

The second cleavage furrow appears about 2 hours after the first (average: 119 minutes). As a rule, it is not quite simultaneous in both blastomeres, one of them being clearly bilobed before the furrow is indicated in the other (fig. 1¹⁰). 14 Minutes later, the furrow has attained its maximal depth; since the 1st furrow has deepened again, too, the 4 blastomeres, which are about equal in size, have rounded off maximally (fig. 1¹¹). Between them, in the centre of the egg, a small space is visible. This stage is followed by a renewed flattening of the cells; at the same time, two opposite blastomeres come into contact at the animal pole, with formation of a short cross furrow (fig. 1¹²), whereas the two other blastomeres meet at the vegetative pole. When the blastomeres have come largely into contact, the central cavity begins to widen; at the same time, small slit-like spaces appear between the blastomeres (fig. 1¹³), which soon coalesce with the central cavity (fig. 1¹⁴). The cleavage cavity, thus formed, widens progressively till it breaks through to the exterior again, and the fluid is expelled, which is accompanied with a considerable contraction of the whole egg (fig. 1¹⁵). This process may be repeated some times before the entrance of the 3d cleavage, which occurs at 210 minutes, about 1½ hours after the second cleavage (fig. 1¹⁶). 6 Minutes later, the maximal rounding off of the blastomeres occurs; the micromeres are most conspicuous at this moment (fig. 1^{17}). They alternate with the macromeres (not clearly visible in the photograph) and are much smaller than these. Then, the outline of the egg rounds off again, with simultaneous enlargement of the cleavage cavity (fig. 1^{18} ^{19}). 25 Minutes after the beginning of the 3d cleavage, the egg has attained a smooth outline again, with a large cleavage cavity bordered by a regular mosaic of cells. Here the period in consideration ends.

In the following description, the phases of development shown in fig. 1 will be referred to as stage 1-19.

2. Nuclear phenomena. The mitotic division of the zygote nucleus begins during the period of elongation of the egg; the spindle forms about 20 minutes before the appearance of the cleavage furrow (RAVEN 1945). Therefore, in the eggs of stage 1 the nuclear division has nearly been completed; it is in the late anaphase or early telophase. The spindle is situated beneath the animal pole plasm at the animal pole. The asters at the ends of the spindle are large, but rather inconspicuous. In the spindle equator, the spindle fibers are somewhat thickened, so that a kind of incomplete partition wall between the two halves of the spindle is formed. When the chromosomes have reached the spindle poles, they begin to swell into little vesicles, each representing, probably, a single chromosome.

In the next few minutes, the asters vanish altogether, so that they are no longer visible in the eggs of stage 2. The swelling of the karyomeres continues (fig. 2). By the deepening cleavage furrow, the spindle is pushed further into the interior of the egg; the karyomeres, however, remain behind in the neighbourhood of the animal pole. In this way, the spindle remnant is displaced with respect to the cleavage nuclei in a vegetative direction; it remains visible till stage 5, where it is found connected with the interblastomeric wall at a considerable distance from the nuclei. At the same time, it appears strongly compressed in the region of its equator; here, a distinct "mid body" may be formed in these late spindle remnants (cf. FRY 1937).

Meanwhile, the karyomeres of the cleavage nuclei have fused; at first, this fusion is only partial, so that a small number of larger nuclear vesicles is formed (fig. 3); ultimately, however, these vesicles unite to a large, vesicular, polymorphic nucleus (stage 5). Both nuclei are situated just beneath the animal pole, near the interblastomeric wall or the cleavage cavity, which is beginning to appear. They are elongated, their long axis being parallel to the plane of first cleavage.

At stage 7, the cleavage nuclei are in prophase. They show a peculiar appearance, the chromatin being accumulated in the outer, animal half of the large vesicular nucleus, whereas the other half is nearly devoid of chromatin, clear and rather homogeneous (fig. 4). This asymmetrical disposition of the spireme is very characteristic of the prophase nuclei of early cleavage.

The formation of the spindles of the second cleavage division begins, on an average, at stage 8; sometimes, however, the preliminaries of this process may be observed already in eggs of stage 7, whereas, on the other hand, prophase nuclei may be found occasionally till stage 9. Evidently, the nuclear development and the external appearance of the eggs show no strict correspondence; this may, however, partly be due to the complication, brought about by the rhythmical process of swelling and contraction of the cleavage cavity during these stages.

The formation of the spindle is preceded by the appearance of small asters at opposite ends of the cleavage nucleus; they are situated close to the nuclear membrane, often in a small indentation of the latter. Then, the membrane disappears in the neighbourhood of the asters, the astral rays penetrate into the nucleus and the first spindle fibers appear as coarse fibrillae crossing the nuclear space from one aster to the other. The spireme, which is rather slender at this moment, is at first irregularly disposed throughout the nucleus; soon, however, the chromosomes contract and arrange themselves in the spindle equator. Meanwhile, the asters have grown; a "central body" appears, while the astral rays extend in the cytoplasm. In the late anaphase, the asters have got their maximal size; then, they vanish rapidly. At stage 10, the telophase is attained. In the spindle equator, thickenings of the spindle fibers are formed, as in the first cleavage. The chromosomes swell into karyomeres. Again, the spindle remnants are pushed by the cleavage furrows to the vegetative side, whereas the karyomeres remain in the neighbourhood of the animal pole; the spindle remnants remain visible till stage 13.

The karyomeres unite progressively to a polymorphic vesicular nucleus; this process is completed at stage 13. At the next stage, the nuclei are in prophase; they have the characteristic appearance with eccentric accumulation of the chromatin in the outer half, as described above.

The formation of the spindles of the 3d cleavage begins at stage 14-15; again, as in the preceding cleavage, there is no strict correspondence between the outward appearance and the nuclear stage; a similar explanation may be given here, on account of the rhythmical expulsion of fluid from the egg.

When the furrows of the 3d cleavage appear at stage 16, the nuclei are in late anaphase or early telophase. The spindle remnants remain visible till stage 18; the karyomeres unite at stage 19 to a polymorphic resting nucleus, which soon transforms into a prophase nucleus with eccentric disposition of the spireme. Whereas in the 2- and 4-cell stages, when the chromatin accumulated in the animal half of the prophase nuclei, it could not be made out whether it is directed by the animal-vegetative polarity of the egg or by a directive influence working from the egg surface inwards, in this stage it is evident that the latter supposition is right: in the nuclei of the macromeres, which are situated no longer near the animal pole of the egg, but near the egg equator, the chromatin is accumulated in the outer, not in the animal half. Evidently, it is attracted by a force working from the surface (or repelled by one in the inverse direction).

3. The cytoplasm. In the eggs of stage 1, a special protoplasm covers, in the form of a narrow layer of uniform thickness, which is rich in β-granules (i.e. granules of proteid yolk, staining red with eosin, blue in azan preparations, cf. Raven & Bretschneider 1942; Raven 1945), the vegetative and equatorial sides of the egg. In a previous paper (Raven 1945), I have called it the ectoplasm; it is, however, better to reserve this name for another substance. Therefore, we will call this outer protoplasmic layer of the uncleaved egg and of the early cleavage stages in future "subcortical plasm". At the animal side, it passes gradually into the animal pole plasm, which forms a broader layer of dense protoplasm, containing many α-granules (i.e. small granules, staining violet with iron haematoxylin, red in azan). The remaining part of the egg is composed of protoplasm, having a vacuolar structure, with coarse γ-granules (black with iron haematoxylin, orange red with azan) in the vacuoles, whereas α- and some β-granules are found in the meshes between the vacuoles. It is the "inner plasm", and corresponds to the substance described as "endoplasm" in my previous paper. Only that part of the inner plasm, which surrounds the nuclei, is somewhat denser, without or with only a few vacuoles.

Externally, the egg is surrounded by a rather firm plasmatic lamella, the vitelline membrane. In the neighbourhood of the animal pole, this membrane is split into two parts, one adhering to the egg surface, whereas the other runs externally to the second polar body, which is enclosed, in this way, between the two lamellae. The first polar body, on the other hand, lies entirely outside the membrane.

When the first cleavage furrow indents the animal pole of the egg, it divides the animal pole plasm into two equal parts, each belonging to one blastomere. The subcortical plasm bends inwards with the cleavage furrow; so does the vitelline membrane (fig. 2). At stage 4, when the egg is constricted maximally, the two nearly spherical blastomeres are both surrounded by a complete external layer, consisting of vitelline membrane and subcortical protoplasm; they are in touch in one point only. Then, when the blastomeres flatten against each other, the vitelline membrane lamellae covering their adjacent sides fuse into a single plasmatic partition wall between the blastomeres; it is covered at both sides by a layer of subcortical plasm.

The processes which lead to the formation of the cleavage cavity will be described below.

At stages 7-9, when the spindles of the 2d cleavage division are formed, the perinuclear accumulation of dense protoplasm comes into contact with the animal pole plasm and blends with it into a common mass, in which the two components cannot be distinguished; when the division is completed, however, they are separated again by a layer of vacuoles. At the beginning of the 3d cleavage division, the animal pole plasm and the perinuclear plasm unite once more. At the same time, the subcortical plasm, which has hitherto remained rather uniform in thickness, concentrates markedly in the animal part of the cells and fuses with the above-mentioned protoplasmic condensation. In this way, the animal half of each of the four cleavage cells is filled by a common mass of dense protoplasm, rich in α- and β-granules, but poor in γ-granules and vacuoles. This mass is divided by the 3d cleavage furrow into two nearly equal parts; one of them comes to lie in the micromere, the other occupies the animal half of the macromere.

In this way, the egg substances are distributed rather unequally over the cells at the 3d cleavage. The micromeres consist almost entirely of dense protoplasm, rich in α- and β-granules (fig. 8); γ-granules and vacuoles are restricted to a narrow layer along the border of the cleavage cavity and the cell boundaries of adjacent cells. In the macromeres, on the other hand, the dense protoplasm is concentrated in the animal half, where it surrounds the nucleus; the remaining part of the cells, with the exception of a thin layer of subcortical plasm, consists of vacuolar protoplasm, with large γ-granules in the vacuoles.

4. The cleavage cavity. The first indications of the formation of a cleavage cavity may be seen in the sections as early as stage 6. The interblastomeric wall, which has been formed, in the manner described above, by the fusion of two vitelline membrane lamellae, appears at first as a single, rather firm membrane in cross section. Now, however, it becomes evident that it is, in fact, a double membrane; in several places, small clefts appear between its two halves (fig. 4). They may remain separated for some time or coalesce to a common, rather narrow lens-shaped cavity.

The interblastomeric wall is covered, at first, at both sides by a layer of subcortical plasm, being somewhat denser than the adjacent inner plasm of the egg (fig. 3). Soon, however, this layer becomes strongly vacuolated; the vacuoles are larger, the interjacent protoplasmic meshes finer than in other regions. By a progressive reduction of the meshes, with confluence of the vacuoles, hyaline zones are formed, bordering the interblastomeric wall and slit-like cleavage cavity. At stage 8, these hyaline zones are well-developed; the protoplasmic meshes are reduced to such an extent that only some fine threads, looking like a coagulum, are left; towards the cleavage cavity, however, a distinct protoplasmic pellicle, which is, in fact, a derivative of the original vitelline membrane, remains always intact. At the same time, these parts of the cell have swollen intensely, so that they protrude as clear prominences into the cleavage cavity, which they may obstruct partially (fig. 5).

Now, the cleavage cavity widens rapidly. At the same time, the hyaline cones described above diminish in size. Evidently, fluid passes through the inner pellicle of these cones towards the cleavage cavity. They may be considered, therefore, as special differentiations serving for the secretion of the blastocoelic fluid. This fluid is no pure water, but contains, probably, proteid substances; in the preparations, the cleavage cavity is partly filled by a fine coagulum.

After the expulsion of the blastocoelic fluid the cleavage cavity is much reduced in size; it does never disappear entirely, however, but a small space remains. During the 2d cleavage (stage 11 and 12), it may come into communication with the exterior by rather wide clefts between the blastomeres. At the next stage, however, these clefts are closed by the extension of the cells. At stage 14, hyaline cones are formed by the four blastomeres, which protrude into the cleavage cavity, reducing it to a small polygonal slit (fig. 6); then, the cleavage cavity is distended considerably by the secretion of fluid from these cones (fig. 7).

At the 3d cleavage, this cycle of events is repeated once more: expulsion of the fluid with reduction of the cleavage cavity; formation of hyaline cones both on the micromeres and macromeres, protruding into the cavity and obstructing it nearly entirely; then, reduction of the cones and widening of the cleavage cavity. At stage 19, the cavity may expand to such an extent that both the micromeres and the macromeres are stretched to rather flat cells lining this cavity.

5. Golgi bodies and mitochondria. At the 2-cell stage, the Golgi bodies are distributed evenly through the cytoplasm, as in the uncleaved egg. They lie in the meshes between the vacuoles; with osmium, they are partly impregnated as a whole, partly they form distinct Golgi systems (cf. HIRSCH 1939).

After staining with Altmann's acid fuchsin, the β- and γ-granules of the egg are orange red. Between them, fine carmine red granules are rather regularly distributed. Evidently, the latter represent the mitochondria; in this respect, my observations are entirely in accordance to those of HIRSCHLER (1918). On the contrary, I cannot share the opinion of GATENBY (1919), who considers the β-granules to be mitochondria; evidently, he has been misled by the rather considerable staining of the β- and γ-granules with acid fuchsin, and has thereby overlooked the true mitochondria, which stain much more intensely.

The mitochondria, demonstrated in this way, are clearly identical with the α-granules mentioned above. This is confirmed by their behavior at the 3d cleavage, when they are accumulated at the animal side of the egg, and, in this way, come to lie mainly in the micromeres and the animal 1/3 of the macromeres, hence in those parts that are composed of the dense protoplasm described above.

6. Cytochemical reactions. a) Fat: At the 2-cell stage,

fat droplets (blackened with osmic acid) of rather equal size are situated in the meshes between the vacuoles. They are distributed rather regularly throughout the egg, leaving free the area of the nuclei. At the 8-cell stage, the macromeres are richer in fat droplets than the micromeres. In the latter, they are mainly found along the border of the cleavage cavity and the cell boundaries; in the macromeres, on the other hand, their density is greatest beneath the subcortical protoplasm, especially in the neighbourhood of the vegetative pole. Thus, the fat droplets are situated chiefly in those parts of the egg that are composed of vacuolar protoplasm; the dense protoplasm, on the contrary, is rather poor in fat droplets.

b) Thymonucleic acid: With the Feulgen reaction the following results have been obtained: In the polymorphic resting and prophase nuclei of stage 5-7 no thymonucleic acid could be demonstrated; the early metaphase chromosomes of stage 8 (2d cleavage spindle) contained only a small quantity of it, being hardly stained in Feulgen preparations. Again, the prophase nuclei of stage 14 are devoid of thymonucleic acid; the same holds true as regards the polymorphic resting nuclei and the prophase nuclei of stage 19. Intermediate stages have not been studied. The observations prove that in these early cleavage stages in the intermitotic phases the nuclei contain no thymonucleic acid. The chromosomes in the 1st polar body, on the other hand, in all these stages possess a moderate quantity of thymonucleic acid.

c) Ribonucleic acid: The distribution of ribonucleic acids has been studied in the 4-cell stage in the manner described by BRACHET (1942). After staining with methylgreen-pyronine after Unna-Pappenheim, the deep red β-granules contrast with a lighter red ground protoplasm; the γ-granules, in the vacuoles, are pink. The subcortical plasm, with its abundance of β-granules, is much more deeply coloured than the inner plasm. A preliminary treatment with ribonuclease takes away the colouration of the hyaloplasm and the β-granules; the γ-granules, however, remain stained. It follows from these observations that free ribonucleic acids are present in the cytoplasm, while another part of these substances is bound to the β-granules.

d) Sulfhydril-compounds: the reaction with alkaline sodium nitroprussiate in the manner described by RIES (1937) was positive both at the 2-cell and the 8-cell stage. In either case, it was most obvious in the cytoplasm immediately surrounding the nuclei. In sections prepared according to the method of Chèvremont & Frédéric (1943), the cytoplasm reacts weakly positive. The egg cortex shows a much more heavy staining. The nucleoplasm remains colorless.

e) Phenolases: With the M-nadi oxidase reaction small granules of indophenol blue are formed, distributed regularly on the egg surface; at the 8-cell stage, no difference between micro- and macromeres could be discerned.

f) Peroxidases: In the reaction with benzidine and H_2O_2 small blue granules were produced, distributed evenly on the egg surface; no difference between micro- and macromeres at the 8-cell stage was found.

7. Vital staining. In general, the results of the vital staining experiments with eggs at the 2-8 cell stage did not differ from those with uncleaved eggs (cf. Raven 1945, p. 113). A differential staining has only been obtained with brilliant cresyl violet: At the 8-cell stage, the micromeres and the animal side of the macromeres become violet, whereas the vegetative side remains yellowish. Evidently, the dense protoplasm of the animal half has a greater affinity towards the stain than the vacuolar protoplasm.

8. Summary. The period described in this chapter is characterized especially by the rather irregular sequence of swelling and contraction of the cleavage cavity, which is correlated but loosely with the rhythm of the cleavage divisions. The blastomeres absorb water from the exterior, and secrete it by means of special "secretion-cones" into the cleavage cavity, from which it is expelled at irregular intervals to the exterior. We may guess that this current of water flowing incessantly through the egg is of great importance for the respiration and the excretion of waste-products. Moreover, it indicates the narrow interrelations existing already at this time between the egg and the surrounding egg capsule fluid, which will become of considerable interest during further development.

As to the distribution of substances in the egg, this remains at first the same as it was at the end of the uncleaved stage. In the first 2 cleavages the egg substances are distributed in a purely passive way over the blastomeres. Therefore, the first 4 blastomeres show, as far as could be determined, the same composition. However, at the 3d cleavage an unequal distribution of substances takes place. This cleavage is preceded by the accumulation, at the animal side of the blastomeres, of a very dense protoplasmic mass; it arises by the confluence of 3 components, viz., 1. the animal pole plasm, 2. the perinuclear protoplasm, and 3. the major part of the subcortical plasm. In consequence of this origin, the dense protoplasm is very rich in α-granules (mitochondria) and β-granules, whereas the remaining part of the cytoplasm contains especially the vacuoles with γ-granules and the fat droplets. In this way, at the 8-cell stage a rather unequal distribution of the egg substances has occurred. The micromeres consist nearly entirely of dense protoplasm and are very rich in mitochondria and β-granules, whereas the macromeres are composed to a large part of vacuolar protoplasm with γ-granules and fat droplets.

II. Further cleavage

1. External appearance. The cell lineage of *Limnaea stagnalis* has not been studied in detail. As far as my observations go, it corresponds in a large measure to that of *Planorbis* and *Physa*, as it has been studied by HOLMES (1900) and WIERZEJSKI (1905); however, it has to be taken into account that these last-mentioned forms are sinistral, whereas *Limnaea* is dextral, so that its cleavage is symmetrically reversed in comparison with theirs. Moreover, small divergences may occur, especially at later stages of cleavage; they are, however, of no great importance and can only be demonstrated by a special investigation. In this paper, I will restrict myself to the histological and cytochemical changes accompanying cleavage.

2. Nuclear phenomena. During the first cleavages, the evolution of the nuclear apparatus is especially characterized by the following peculiarities: 1. The mitotic spindles are provided with asters, appearing in the prophase stage as small structures close to the nuclear membrane, growing rapidly by the extension of the astral rays into the surrounding cytoplasm and the formation of a "central body", attaining their maximal size at the late anaphase stage, then disappearing quickly. 2. The telophase chromosomes swell into karyomeres, which remain separate at first; they do not fuse till shortly before the beginning of the next mitosis. Hence, during the major part of the intermitotic phase a karyomere nucleus exists. 3. The single nucleus, formed by the fusion of the karyomeres, retains the traces of its origin in its irregular, polymorphic shape, which it preserves till the prophase

of the next division. 4. The prophase nuclei are characterized by the unilateral accumulation of the chromatin in the outer half of the nucleus.

These peculiarities of the nuclear cycle persist till about the 16-cell stage; then, rather abruptly a change occurs. From this stage on, karyomere nuclei have no more been observed; the resting nuclei show a rather regular round or oval outline. Evidently, the restitution of the nucleus after mitosis takes place in another way now than in the earlier phases of cleavage. Furthermore, with the decrease of cell size, the asters diminish in importance; at a stage of about 40 cells, only the mitotic spindle of the primary mesomere shows small asters at both ends; the other mitoses are anastral. Finally, the unilateral accumulation of chromatin in the prophase nuclei has not been observed beyond the 24-cell stage.

Another change in the structure of the nuclei is still more important. At earlier phases, the resting nuclei contain many scattered small granules of nucleolar substance; with the progress of cleavage, the number of nucleoles diminishes, but their size increases considerably. At the 24-cell stage, each nucleus contains, as a rule, 2 or 3 nucleoli; at the stage of about 40 cells, most nuclei possess only 1 or 2 nucleoli (fig. 9). The structure of these nucleoli is very interesting. They consist, as a rule, of two parts, having different properties. The inner part stains red with eosin; the outer, which is rather irregular in shape, sometimes completely surrounding the internum, in other cases forming a cap or interrupted ring upon the latter, stains black with iron haematoxylin. Evidently, the nucleoli are the site of an intense metabolic activity. It could be demonstrated cytochemically that both parts contain ribonucleic acid, but no thymonucleic acid. With the beginning of prophase, the nucleoli disappear.

During later stages of cleavage, the size of the nucleoli increases considerably. At the same time, their shape becomes more regularly spherical. In many cases, their composition of two parts is still very distinct; the internal part is often very conspicuous by its different refractive index.

At the stage of about 120 cells, a new phenomenon makes its appearance. Apparently, in many nuclei whole nucleoli break through the nuclear membrane and come to lie in the cytoplasm, where they soon fragment into smaller pieces, which are lost among the yolk granules. Though it is difficult to prove such a process with absolute certainty, the pictures obtained of nucleoli under way in a break of the nuclear membrane or lying just outside the nucleus can hardly be interpreted in another way.

We are obliged to conclude, therefore, that the nuclei, and especially the nucleoli, evidently play an important part in the metabolic processes of the cells during this period.

3. The cytoplasm. At the time of the 3d cleavage, the cytoplasm of the egg consists of 2 different portions: a mass of dense protoplasm with many α- and β-granules on the animal side, vacuolar protoplasm with γ-granules and fat droplets on the vegetative side. The 3d cleavage divides these 2 substances unequally over the cells, the micromeres consisting mainly of dense protoplasm, whereas the macromeres are composed to a large part of vacuolar protoplasm; both, however, receiving also a part of the other substance (fig. 8).

This unequal division of both substances repeats itself at the next cleavages; evidently, at each division both daughter cells receive a part of both, be it in unequal amounts. Hence, at a stage of about 40 cells, all blastomeres contain both kinds of protoplasm, but in different proportions (fig. 9).

In all cases, the dense protoplasm occupies the outer zone of the cells, the vacuolar protoplasm the inner part. Therefore, we will call them ectoplasm and endoplasm, respectively; it should be noted, however, that these denominations have been used in my previous paper (1945) in a somewhat different sense, indicating the "subcortical plasm" and "inner plasm" of the uncleaved egg, respectively.

At the stage of about 40 cells, the most animal blastomeres consist nearly entirely of dense, deeply stained ectoplasm, very rich in mitochondria; only the innermost portions of the cell are composed of vacuolar endoplasm. In embryos with a wide cleavage cavity, the ectoplasmic parts of the cells are distended in the form of rather flat plates, whereas the endoplasmic portions protrude as slender processes into the cavity (fig. 9).

The cells, situated supraequatorially in the egg, differ from these animal blastomeres by a greater amount of endoplasm, almost equalling that of the ectoplasm. Again, the endoplasmic parts protrude into the cleavage cavity with large granular heads.

Finally, in the cells of the vegetative half of the egg the amount of endoplasm surpasses many times that of the ectoplasm. Hence, it can be said that the relative amount of endoplasm in the blastomeres increases from the animal to the vegetative pole, whereas the relative amount of ectoplasm decreases in the same direction (fig. 9).

It is very interesting to note that in all blastomeres the nucleus is situated at the boundary between ecto- and endoplasm (fig. 9). Thus, in the animal blastomeres it lies close to the inner surface of the cell, separated from it by the thin layer of endoplasm only; in the supraequatorial cells it is situated about half way between the outer and inner end of the cell; finally, in the vegetative blastomeres the nucleus lies near the outer surface, immediately beneath the rather narrow layer of ectoplasm. This constant position of the nucleus between the two parts of the cytoplasm, which is found throughout cleavage, makes it likely that it has to play an important part in the interactions between ecto- and endoplasm.

The nature of these interactions is indicated by the following observations: At the 40-cell stage, the "vacuolar" protoplasm (endoplasm) is less strongly vacuolated than at the 8-cell stage. The γ-granules, which it contains, are large and numerous; unlike the 8-cell stage, they are only partly situated within the vacuoles; most of them are found in the meshes between the vacuoles. In the next stages, the vacuolization of the endoplasm decreases further; at the same time, the number of γ-granules has been augmented moderately.

What is the mode of origin of these γ-granules, arising anew during cleavage? In iron haematoxylin preparations, it has the appearance that they arise by fragmentation of nucleoli extruded into the cytoplasm; the identical staining of nucleoli and γ-granules with iron haematoxylin seduces to such an interpretation. With azan, however, the nucleoli stain deep red, the γ-granules more orange red; this makes a direct fragmentation of nucleoles into γ-granules unlikely. This hypothesis becomes, furthermore, altogether untenable by the results of the cytochemical reaction upon ribonucleic acids; whereas the nucleoli contain a high concentration of these substances, the γ-granules are only poor in ribonucleic acid.

We have to look, therefore, for another source of the substances giving rise to the formation of γ-granules. In this connection, the behaviour of the β-granules is of interest. At the 8-cell stage, these granules are very abundant especially in the dense protoplasm, in smaller number also in the endoplasm. At the 40-cell stage, in the endoplasm scattered β-granules are found between the γ-granules; in the ectoplasm, however, no distinct β-granules can be recognized. The whole ectoplasm is eosinophil and rather heavily stained; one gets the impression that the β-granules have been dissolved in the hyaloplasm. In the next stages, the β-granules in the endoplasm disappear, too. Then, the formed proteid yolk consists entirely of coarse γ-granules.

Still another phenomenon is of importance in this respect. Already at the 40-cell stage, numerous small vacuoles appear in the ectoplasm, being stellate in shape or irregularly branched, and, probably, communicating with one another by very fine canaliculi (fig. 9). Their contents are strongly eosinophil. With all stains used, its colour corresponds to that of the egg capsule fluid surrounding the egg. We may conclude from these observations that the ectoplasmic vacuoles contain albumen taken in by the cells from the surrounding egg capsule fluid. These albumen vacuoles are found at the 40-cell stage especially in the animal half of the egg; in the vegetative blastomeres, they are far less conspicuous or are lacking altogether. At the 60-cell stage, the albumen vacuoles in the ectoplasm have grown larger; at the same time, their shape is more regular, round or oval. At the animal side of the egg they are larger than at the vegetative side. At the 120-cell stage, these vacuoles have still increased in size; they occupy a large part of the volume of the ectoplasm. At the same time, their number has diminished by the coalescence of several small vacuoles to larger, polymorphic vesicles. Still, they are at the animal side larger in size and in number than at the opposite side of the egg.

It is difficult to decide whether the albumen is digested by the cells. No indications of a digestive action could be observed; on the other hand, in view of the fact that at a somewhat later stage of development a consumption of albumen takes place on a large scale, it seems improbable that the intake of albumen by the cells is wholly without importance.

Summarizing, it can be stated that a moderate augmentation of the γ-granules corresponds in time to a dissolution of the β-granules and an intake of albumen by the cells. It seems likely that these processes are linked in some way or other; probably, the proteid substances originating from one of the last-mentioned processes, or from both, are temporarily precipitated in the form of γ-granules. However this may be, it is clear that important metabolic processes, especially concerning the proteid yolk substances, are going on in the egg during cleavage; considerable interactions between ecto- and endoplasm are implicated by them. Therefore, the constant position of the nucleus at the boundary between these plasms is very important; it indicates that the nucleus plays a part in the proteid metabolism of the cells.

Some special differentiations have to be mentioned. At the 40-cell stage, the M-blastomere, which is in mitosis, shows no striking peculiarities distinguishing it from other vegetative blastomeres; probably, however, in consequence of the direction of the division by which it is formed, it is from the beginning nearly or altogether devoid of ectoplasm. Perhaps, this may account for some of its special properties, e.g. the tendency of the mesoblasts to withdraw from the surface into the interior of the egg. A short time afterwards, at the 60-cell stage, the 2 M-blastomeres strike by a somewhat darker protoplasm and a great abundance of γ-granules; at their conical vegetative ends, reaching to the outer surface of the embryo, a special, very dense protoplasm is accumulated, staining blue violet with iron haematoxylin and eosin, orange brown in azan-stained preparations. At later cleavage stages, all cells of the mesoderm are recognizable by their dark stained cytoplasm rich in γ-granules.

At the 40-cell stage, near the central end of each of the cells of the 4th quartette (including the M-blastomere) a peculiar dark body is found (fig. 9). It is oblong, mostly somewhat conical in shape, and stains black with iron haematoxylin, deep red with azan. The cytochemical reaction upon ribonucleic acid shows that it contains a high concentration of this substance.

These bodies agree in many respects with similar corpuscles, described by WIERZEJSKI (1905) in *Physa*, and called "Ectosomen" by him. Here, they arise at the 3d cleavage as granules in the vegetative asters of the cleavage spindles, which are displaced towards the surface at the vegetative pole, where they remain along the vegetative crossfurrow till the 24-cell stage, when all blastomeres come into contact in the centre of the egg, where a vacuolated space is formed. At this stage, the ectosomes move to the central extremities of the macromeres, after which they disappear altogether.

In *Limnaea*, at the 16-cell stage large dark granules are present, scattered throughout the cytoplasm of the macromeres. At the 24-cell stage, they are accumulated at the central ends of the macromeres, where they fuse into irregular heaps, ultimately forming the single bodies described above; at the next division they pass into the cells of the 4th quartette. At the 60-cell stage, in some cases a few of these corpuscles are still visible; their occurrence is, however, less constant and regular than at the former stage. At later cleavage stages they have not been found. As to the way in which they disappear no observations have been made.

At the 120-cell stage, a special kind of fine granules, staining light blue in azan, have been observed at the central extremities of some vegetative cells; it is difficult to decide, whether they have anything to do with the above-mentioned bodies, lying at the same place at earlier stages, though their different staining reaction speaks against such a derivation.

A further kind of rather enigmatical structures has to be recorded. At the 40-cell stage, at the surface of some blastomeres small, conical or hemispherical, vesicular projections could be observed (fig. 9). At the 60-cell stage, they have developed further. Now, they have, in their most completed form, the appearance of small thickened rings of variable diameter, projecting slightly above the surface of the cells, and surrounding a somewhat crater-like field. The ringlets stain black with iron haematoxylin, red with azan; the central area remains colourless. In total, 8-12 of such rings were observed; they are arranged in 4 equatorial groups, along 4 meridians of the egg deviating 90° each. As far as could be made out, they belong to cells of the 2d quartette. At the 120-cell stage, their number has increased considerably; 40-60 of such ringlets are observed in most eggs. Still, they lie in 4 groups cross-wise around the egg axis; the number of rings in each of these groups is, however, not equal, one of them being much larger than the other. The general appearance of the rings has not changed; their size varies considerably. Some of them have projected somewhat further above the surface; moreover, hemispherical and conical structures are still present between them, probably representing stages in their formation (fig. 10).

As to the nature and significance of these ringlets, I have come to no conclusion. I know of no other structure with which they could be compared. In some cases, I got the impression that the

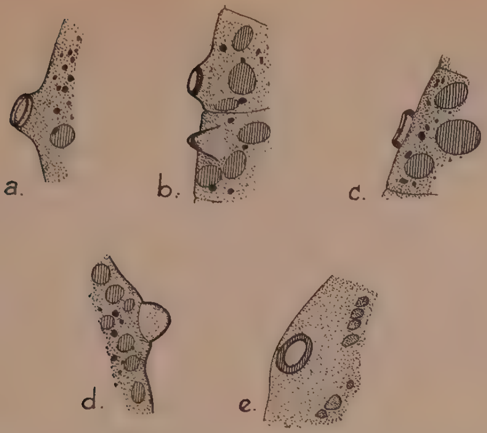

Fig. 10. Thickened ringlets on the surface of the blastomeres of a 120-cell stage of *Limnaea stagnalis*.

vitelline membrane surrounding the egg is attached rather firmly at the place of the ringlets; it may be that they are related to this membrane. Another explanation is put forward by the fact that the formation of the rings corresponds in time to the absorption of albumen by the cells; it could be assumed that they represent inlets destined for the ingestion of the egg capsule fluid. I could observe, however, no constant relation between the ringlets and the albumen vacuoles of the cells; furthermore, many cells contain albumen vacuoles although they possess no ringlets. The question of the significance of these structures must, therefore, remain open.

4. The cleavage cavity. The cyclic transformations of the cleavage cavity have not been studied, in this phase, with as much accuracy as during the first cleavages. That such transformations do actually occur is indicated by the observation that embryos of the same stage may have cleavage cavities of very different width. On the other hand, the sequence of expansion and contraction of the cleavage cavity is correlated more or less with the rhythm of cleavage divisions; therefore, for particular stages of the cleavage process a special conformation of the cleavage cavity is characteristic. This is most evident at the 24-cell stage, when all blastomeres meet with conical projections at the centre of the egg, the cleavage cavity disappearing altogether, as has been described already by Wierzejski (1905) in *Physa*. At

the place of junction a central area of protoplasm, free of yolk granules and mitochondria, is formed; it belongs chiefly to the animal blastomeres, but extends also over the tips of the equatorial and vegetative cells. Probably, this central mass of protoplasm corresponds to the vacuolated area described by WIERZEJSKI at his place; in *Limnaea*, however, it is not vacuolated.

The shape of the cavity at more advanced cleavage stages is very irregular; often, it extends with narrow slit-like projections far between the blastomeres. I may refer to the accurate descriptions of these phenomena in *Limax* in the papers of KOFOID (1895) and MEISENHEIMER (1896), which agree entirely with those observed in *Limnaea*.

At the 16-cell stage, hyaline zones along the inner borders of the blastomeres, corresponding to the "secretion-cones" found in earlier stages, were observed. At later stages, no such structures have been found.

5. Golgi bodies and mitochondria. At the 24-cell stage, Golgi systems of different size are found scattered between the yolk granules. They possess a strongly-developed internum, which is surrounded by a very thin, often more or less discontinuous externum. The internum has the same aspect as the surrounding large yolk granules. These observations suggest that the Golgi systems assist in the transformation of the yolk granules. Moreover, centrally to the nuclei a Golgi field with fine black granules and rods of praesubstance is present.

At the stage of about 95-100 cells, only these Golgi fields, immediately adjacent to the nuclei and situated at their inner side, consisting of a loose network of fine black granules and rods, are found. Some fine black granules (praesubstance?) are present also in the rest of the cell, between the yolk granules; no Golgi systems have, however, been observed at this stage.

These observations contradict the assumption of GATENBY (1919) and HIRSCHLER (1918) that the Golgi systems remain altogether passive during cleavage. These authors have assumed without further discussion that the Golgi systems found by them in the cells of the gastrula are the same as those observed at early cleavage stages. My observations awake the suspicion, however, that the former belong to a new generation of Golgi systems derived from the praesubstance in the Golgi fields of cleavage cells, whereas the Golgi systems of early cleavage stages are used up in the transformation of the yolk.

At the 24-cell stage, the mitochondria are regularly distributed between the β- and γ-granules. Like these, they leave free the area of the "central protoplasm" mentioned above. At the 40-cell stage, it is clear that their density is much greater in the ectoplasm than in the endoplasm of the cells.

6. Cytochemical reactions. a) Fat: At a stage of about 45 cells, with osmic acid fat droplets of rather equal size are found especially in the endoplasm; the ectoplasm, on the other hand, contains only sporadically some fat droplets. Therefore, the vegetative blastomeres, with their abundance of endoplasm, are by far richer in fat than the animal cells; in the latter, the fat droplets are nearly entirely restricted to a narrow zone between the nucleus and the cleavage cavity.

b) Glycogen: At the 24-cell stage, the localization of glycogen has been determined in preparations stained with Best's carmine. Scattered granules of glycogen were observed in the cytoplasm, especially along the cell walls; a dense accumulation of these granules was found in the central protoplasm, described above as characteristic of this stage. The accumulation of glycogen granules on the outer surface of the cells, beneath the vitelline membrane, and on the surfaces bordering the cleavage cavity, may be due to a secondary translocation of glycogen during the alcohol fixation.

The observation that glycogen granules are accumulated in the central protoplasm, which is free of mitochondria, proves that, at least at this stage, the glycogen is not bound to the mitochondria (α-granules), as has been assumed in a previous paper to be the case in the uncleaved egg (Raven 1945).

At a stage of about 70 cells, with the iodine reaction on whole eggs a rather weak brown granular colouration of the cells appeared. At the vegetative side, the cells of the 4th quartette (except the M-blastomeres) stained rather heavily. With saliva, the brown granules disappeared.

c) Thymonucleic acid: At the stage of about 70 cells, the Feulgen reaction gave the following results: The resting nuclei do not contain thymonucleic acid; in the prophase stage, a distinct chromatin thread, staining light violet, appears; the colour increases in intensity and becomes more red as the metaphase progresses; finally, the late anaphase and telophase chromosomes are deep red in colour. Evidently, thymonucleic acid is present only during mitosis, and its concentration increases towards the telophase stage, whereafter it suddenly disappears.

d) Ribonucleic acid: The ribonucleic acid test has been performed at a stage of about 40 cells, and furnished the following results: In the nuclei, only the nucleoli contain ribonucleic acid, in large quantity. The cytoplasm and β-granules both contain ribonucleic acid; its concentration seems to be greater in the ectoplasm than in the endoplasm. The dark bodies in the cells of the 4th quartette, described above, have a strong affinity towards pyronine; their colouration is as heavy as that of the nucleoli; like these, they are colourless after treatment with ribonuclease. Evidently, these bodies contain large quantities of ribonucleic acids.

e) Sulfhydril compounds: The reaction with alkaline sodium nitroprussiate gave a distinct colouration of all cells. At earlier cleavage stages, where the cells are still rather coarse, a localization of the reaction in the neighbourhood of the nucleus was obvious. No difference between the animal and vegetative side has been observed.

With the method of CHÈVREMONT & FRÉDÉRIC, a weak colouration of the cytoplasm appears. It is somewhat stronger in the ectoplasm. The nucleoplasm remains colourless, but the nucleoli are rather heavily stained.

f) Phenolases: With the M-nadi oxidase reaction, regularly distributed blue granules appear in all blastomeres. No differential reaction of the cells could be observed.

g) Peroxidases: The reaction with benzidine and H_2O_2 was positive in all cells; no differential reaction.

h) Iron: Non-masked iron is found in all cells in the cytoplasm in granular form. ¹) The nuclei do not contain iron.

7. Vital staining. The eggs were stained by transferring them to a diluted dye solution while enclosed in their capsules. Eggs delivered from their capsules and placed in tap water, soon show a hydropic swelling, accompanied with a loosening of the coherence of the cells. With various vital stains, different results have been obtained.

a) With brilliant cresyl violet, the results varied with the procedure of staining. When the eggs were placed in a weak, but distinctly coloured solution of the dye, in 10-15 minutes a clearly

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¹) The iron determinations have been executed by Miss E. EXALTO with the Prussian blue method after TARTAKOWSKY. It is a pleasure to thank Miss EXALTO for putting her results at my disposal.

differential staining occurred. At the 16-cell stage, the animal blastomeres showed an elective violet colouration. At later stages, in the animal blastomeres the dye is bound in the form of red granules. In some eggs, colour differences between individual cell generations have been observed, the apical cells having a brownish yellow tint, whereas the trochoblasts were violet and the arms of the cross showed a red granular staining; these results could, however, not be reproduced regularly and may have occurred incidentally.

Different results were obtained, when the eggs were left for 24 hours in a still more diluted solution of the dye. Now, all blastomeres were stained in the same tint; perhaps, the colouration of the animal blastomeres was somewhat stronger, but the difference was slight.

When such eggs were placed under a sealed cover slip, even after 20 hours no reduction of the dye occurred.

With high magnification, it could be seen that brilliant cresyl violet stains diffusely the cytoplasm, especially the ectoplasm; moreover, small granules, lying in the albumen vacuoles, are heavily stained in a dark violet tint. The yolk granules remain colourless.

b) With neutral red, a differential staining of the animal blastomeres could be obtained also with the "slow" staining method in a very diluted dye solution. In the equatorial and vegetative blastomeres the colouration is hardly perceptible, whereas the animal cells show a distinct red colouration. With high power, in the stained cells orange red vacuoles are observed, lying between the unstained yellow yolk granules; chiefly, they are restricted to the ectoplasm. Evidently, we have to do with the albumen vacuoles of the cells.

c) With nile blue hydrochloride and cresylechtviolet, the eggs stain rather heavily. In the former, beside a green colouration of the whole egg very dark granules are visible. With high magnification, they appear to be deep blue ectoplasmic vacuoles similar to those stained with neutral red. Moreover, the yolk granules have got a green colour.

f) Methylene blue did hardly stain the eggs. When whole egg capsules were placed in a weak solution of methylene blue, the egg capsule fluid became deep blue; the eggs, however, remained colourless. Under a sealed coverslip, no discolouration of the egg capsule fluid occurred, even after 2 days.

Contrary to intact eggs, those swollen in tap water stain rather heavily. In these postvitally stained cells, no elective absorption of the dye by distinct cell structures can be observed; evidently, it is a diffuse staining. Only the nucleoli have become distinctly greenish blue.

e) Similar results have been obtained with Janusgreen. Intact eggs and cells remain colourless or nearly so; eggs damaged by swelling in tap water stain immediately. Often, the disintegration process begins with the swelling of one or a few cells; these injured cells are easily recognizable as green spots in an otherwise colourless egg.

f) With trypan blue and indigocarmine, the eggs were stained hardly or not at all. In whole egg capsules, trypan blue gave an intense colouration of the egg capsule fluid; the eggs remained colourless.

8. Summary. The main characteristics of this period of development are: 1. a further differential distribution of substances over the cleavage cells; 2. transformation processes of the yolk.

The dense protoplasm and vacuolar plasm, occupying the animal and vegetative side, respectively, at the 8-cell stage, are distributed in a regular way over the blastomeres during cleavage. The dense protoplasm, being especially rich in β-granules and mitochondria, forms the ectoplasm of all cells; the vacuolar protoplasm, containing most fat droplets, forms the endoplasm. The relative amount of ectoplasm decreases from the animal to the vegetative side; that of the endoplasm decreases in inverse direction. In this way, a gradual variation of the proportion between ecto- and endoplasm is brought about. The M-blastomeres, which possess from the outset a particular small amount of ectoplasm, withdraw from the surface and soon acquire special staining properties. Furthermore, the blastomeres of the 4th quartette (mesomere and 3 entomeres) are characterized by peculiar dark bodies rich in ribonucleic acid, which are, probably, dissolved in the cytoplasm at further development. Moreover, the 3 entomeres of the quartette are, probably, richer in glycogen than the rest of the egg. Finally, the formation of thickened ringlets on the surface of 4 equatorial groups of cells, probably belonging to the 2d quartette, has to be mentioned here.

The transformation of the yolk consists in a dissolution of the

β-granules, an ingestion of albumen from the surrounding fluid, and a simultaneous augmentation of the γ-granules. Probably, the nuclei play a part in these processes, as is indicated by their position in the cells, and by a striking activity of the nucleoles, ending, probably, in their extrusion into the cytoplasm. Furthermore, the Golgi bodies of the egg seem to assist in these transformation processes. Whether the glutathione, accumulated in the neighbourhood of the nuclei, plays a part in these processes, too, is at this moment difficult to decide.

III. Gastrulation

1. External appearance. The course of the gastrulation process in the aquatic Pulmonates has been sufficiently described in the papers of RABL (1879), HOLMES (1900) and WIERZEJSKI (1905). Therefore, I will restrict myself to the histological and cytochemical changes.

2. The nuclei. The size of the nuclei shows considerable variations. However, no regular differences between the nuclei of ectoderm, entoderm and mesoderm cells have been observed. Each nucleus contains 1-2 nucleoles, of variable size. In iron haematoxylin-eosin preparations, the nucleoli are black; in sections stained with azan, however, their colour differs very much. As a rule, they are deep red or orange red; besides, however, violet and even greenish nucleoles have been observed in the same preparations. The larger nucleoles often contain a highly refractive droplet (fig. 11). That this is no mere fixation artifact, is proved by the fact that it is obvious also in cells stained postvitally with Janusgreen. The extrusion of nucleoles into the cytoplasm is indicated in many cells.

3. The cytoplasm. At this stage, a clear distinction can be made between the three primary germ layers. This is a consequence of the segregation processes studied in the preceding chapter. The mesoderm consists of the descendants of the M-blastomere, which is formed already at a very early cleavage stage (immediately after the 24-cell stage) by an oblique division of the posterior macromere, which causes it to be nearly or entirely devoid of ectoplasm; according to HOLMES (1900) and WIERZEJSKI (1905), other mesodermal elements are derived in a similar way from the anterior quadrants of the 3d quartette. The entoderm takes its origin from the blastomeres of the vegetative side of the egg, containing a large quantity of endoplasm, but only

little ectoplasm. Finally, the ectoderm is formed by the remaining cells of the embryo, having a larger amount of ectoplasm.

The manner of formation of each of the germ layers accounts for its characteristics. The mesoderm consists of polygonal cells, containing a rather dense protoplasm, which has a great affinity towards protoplasm stains, and contains many large γ-granules.

The formation of the archenteron is brought about by a peculiar change of shape of the cells at the vegetative pole of the egg. Whereas at previous stages the latter are conical with base turned outwards, now a reduction of their outer surface occurs, while their transverse diameter increases more inwards. In this way, they get the form of an inverted cone or wedge, with point directed outwards (fig. 11). This change of form leads to the invagination of the archenteron.

By the contraction of the outer part of the cell, the ectoplasm is pushed inwards. Hence, the height of the ectoplasmic layer increases. The nucleus, which remains near the boundary between ecto- and endoplasm, is, therefore, also displaced more inwards, and comes to lie in the inner half of the cell. The broad inner end of the cell sends forth prolongations in the direction of the ectoderm.

The ectoplasm contains many α-granules (mitochondria) and large albumen vacuoles. In the narrow outer end of the cell, the latter lie, as a rule, in a single row; inwards, their position is more irregular. The endoplasm contains many γ-granules of moderate size.

In many cases, small transparent vesicles have been observed protruding from the cells into the lumen of the archenteron. In the next stage, such vesicles were observed lying free in the albumen filling the archenteron. Probably, they represent secretion products, serving, perhaps, to a liquefaction of the albumen. Nothing more definite could be made out concerning their nature and the manner of their formation.

The ectoderm forms a single layer of cells covering the convex part of the embryo. All cells are composed of ectoplasm, the amount of which increases to the animal side, and endoplasm, which decreases in the same direction. The nucleus is situated at the boundary of both substances. The ectoplasm contains α-granules and albumen vacuoles, which are smaller than those of the entoderm; their size has decreased in comparison to the preceding stages. In the endoplasm, rather large γ-granules are present.

At the animal pole, where a depression is formed opposite the blastopore, a few cells are found, which are distinguished by the presence of extremely big albumen vacuoles (fig. 11). Mostly, they contain one vacuole, the diameter of which largely surpasses that of the nucleus, and a number of smaller ones. The contents of these big vacuoles may show a peculiar picture, being not homogeneous, like that of the smaller albumen vacuoles, but consisting of several dark stained rods lying irregularly dispersed. This may be a mere fixation artifact, but it may also indicate a beginning digestion of the albumen.

The thickened ringlets on the surface of several ectodermal cells, described in the preceding chapter, are still present. Their structure has remained the same. The number of these ringlets has, apparently, decreased somewhat, the maximal number observed being 28. Still, their arrangement into 4 groups can be made out with some difficulty. In whole mounts of gastrulae, fixed in formol and stained with Scharlach R, these ringlets are also visible; here, they have the appearance of little chimneys upon the cells; they are not stained by Scharlach.

4. Cytochemical reactions. a) Fat: In toto preparations of gastrulae, stained with Scharlach R and mounted in glycerine, it is clearly visible that the outer (ectoplasmic) part of the ectoderm cells does not contain fat droplets. The inner mass of the embryo contains much fat, but its precise localization cannot be determined.

b) Glycogen: When early gastrulae are treated with iodine, a brown granular colouration appears. At the animal side, it is most obvious in the cells surrounding the polar depression; at the vegetative side, in a horseshoe-shaped area encircling the anterior border of the blastoporal pit, probably containing the descendants of the cells 4a-4c. Sections stained after Bauer show that this area of glycogen-rich cells extends somewhat into the wall of the archenteron; it is delimited by a sharp boundary from the wedge-shaped entoderm cells near the tip of the archenteron, which are poor in glycogen. The mesoderm cells also contain a small quantity of glycogen only.

c) Thymonucleic acid: In Feulgen preparations it is obvious that the abundance of thymonucleic acid has increased considerably. The resting nuclei, which were completely devoid of it at previous stages, now show different conditions. Besides a few, which are colourless, many resting nuclei possess fine red granules against the nuclear membrane and around the nucleolus. In the mitotic stages, the spireme and chromosomes are stained more heavily than at previous stages.

In the control preparations (stained without preceding hydrolysis), in which the chromatin remains colourless, the nucleoli show a light pink colour. The internal droplet of the nucleoli, however, remains colourless, proving once more that its substance differs from that of the surrounding mantle. In several nucleoli, the internum is situated eccentrically, suggesting that it may break through the external mantle to be extruded into the nucleoplasm.

d. Ribonucleic acid: The ribonucleic acid test gave the following results. The nucleoli contain these acids, with the exception of the inner droplet, which is not stained with pyronine. In the cytoplasm, most ribonucleic acid is found in the ectoplasm of ectoderm and entoderm cells, staining diffusely deep red with pyronine; the albumen vacuoles remain colourless. In the endoplasm, on the other hand, the concentration of these acids seems to be much smaller. The γ-granules show a light orange red colour with pyronine. Therefore, in the mesoderm cells, which do not possess ectoplasm, only the nucleoli contain a considerable amount of ribonucleic acid, whereas the cytoplasm is very poor in this substance.

e) Sulfhydril-compounds: With alkaline sodium nitroprussiate (after RIES, i.e. with fixation of the eggs in trichloracetic acid) a distinct reaction, especially in the entoderm, less strongly also in the ectoderm, was observed. Probably, it was localized mainly around the nuclei. In sections prepared after CHÈVREMONT & FRÉDÉRIC, the cytoplasm and nucleoli show a distinct reaction. In the ectoplasm it is stronger than in the endoplasm; in the entoderm stronger than in the ectoderm.

5. Vital staining. The results of vital staining agree, in general, with those obtained at the preceding stage. The following observations are of particular interest:

a) Neutral red: The neutral red vacuoles in the ectoplasm have grown larger than at the preceding stage, but their number has somewhat diminished; probably, a coalescence of these vacuoles has taken place. They are irregularly distributed throughout the ectoplasm; local accumulations of several vacuoles are observed.

b) In nile blue hydrochloride, beside the accumulation of the dye in ectoplasmic vacuoles, the yolk granules have got a green tint; moreover, in heavily stained eggs small granules between the yolk platelets, probably being mitochondria, are stained in a deep blue colour.

c) In brilliant cresyl violet, the ground protoplasm is diffusely stained; furthermore, the dye is condensed in small rods and granules in the albumen vacuoles of the ectoplasm. The yolk granules are colourless.

d) Methylene blue: Eggs were placed, within their capsules, into a diluted solution of methylene blue at the 2-cell stage. Two days later, when they had reached the gastrula stage, the egg capsule fluid had become intensely blue; the intact eggs had, however, remained practically colourless, only the polar bodies and some dead cells had stained deep blue. Now, the eggs were delivered from their capsules and transferred to well aerated tap water on a slide; their colouration did not increase. Then, the eggs were fixed by heat; no colouration appeared, even after the addition of H_2O_2 or $KClO_3$. When the dead eggs were placed in methylene blue once more, they stained heavily in a few moments.

This experiment proves that the embryos did not contain the dye in its reduced form, even after a prolonged stay in the deeply coloured egg capsule fluid. The failure of the intact eggs to be stained is, therefore, not due to a reduction of the dye by the cells, but, probably, to a relative impermeability of the living protoplasm to the dye or to the lack of cell structures absorbing it.

When treated with rongalite white, the embryos soon show signs of injury (either by the rongalite or only because of the hypotonicity of the medium) by a swelling and loosening of the cells. The cells remain colourless as long as they are intact; swelling and staining of the cells go hand in hand. Evidently, the leucobase shows the same behaviour as the oxidized form of the dye.

e) Janusgreen: When placed in a diluted, slightly acidified solution of Janusgreen in tap water, the cells remain colourless as long as they are intact; as soon as the swelling due to hypotonicity begins, the swollen cells take up the stain. When these swollen and stained cells were observed with oil immersion lens, the following points were noted: The dye is bound to the mitochondria, which are visible as fine bluish green points in the cytoplasm. Moreover, rather large granules (probably the γ-granules) have become yellowish green in colour; they are numerous and large in the internal (ento- and mesodermal) cells, whereas the ectodermal cells contain only few of these granules. The nuclei are clearly visible; the nucleoles are green, with colourless internum. In dividing cells the spindles and chromosomes can be seen; in many of these cells, it is obvious that the γ-granules have accumulated in the plane of the spindle equator. In the course of many hours, no changes are observed in these cells; evidently, the life processes have stopped. We have to do, therefore, with a postvital staining of the cells. No reduction of the dye under a coversllp, even after many hours, has been observed.

6. Summary. This stage of development is characterized by the change of form of the cells at the vegetative pole of the egg, causing the invagination of the archenteron, and bringing about, in this way, a clear distinction between ectoderm and entoderm. No essential changes of the structure of the cells, in comparison to the previous stage, have occurred; only a decrease of the size of the albumen vacuoles in the ectoderm is to be noted, with the exception of the cells forming the centre of the depression at the animal pole, where these vacuoles, on the contrary, have got giant dimensions.

In chemical respect, the most remarkable fact is a considerable augmentation of thymonucleic acid. As a matter of fact, the total amount of this acid increases considerably during cleavage by the multiplication of the nuclei; at this stage, however, its amount increases still more, so that it can be determined also during the resting stage of the nuclei.

The cooperation of the nuclei in the metabolic processes of the cells is indicated also at this stage. Their position at the boundary between ectoplasm and endoplasm remains the same. The nucleoli consists of an internal and external part. The internum is, perhaps, periodically extruded into the nucleoplasm. The externum contains ribonucleic acid, and is surrounded, during certain phases of the intermitotic period, by a layer of thymonucleic acid granules. Probably, whole nucleoli can be extruded into the cytoplasm, which is characterized, in the neighbourhood of the nucleus, by a particular abundance of glutathione. All these facts point to a remarkable metabolic activity of the nuclei.

IV. The beginning of differentiation

1. External appearance. At the end of the gastrulation period, the first signs of histological differentiation make their appearance. Externally, they become obvious by the segregation of the ectoderm into 2 kinds of cells: large, flat and transparent on one hand, small and columnar on the other. The large ectodermal cells occupy a nearly continuous area, in which 3 parts can be distinguished: 1. the head vesicle, formed by the enlargement of the cells situated behind the animal pole of the egg, and occupying a large part of the upper half of the embryo, 2. the velum or prototroch, forming a double row of ciliated cells extending from the ventral side, immediately in front of the mouth, to the dorsal side, where it unites at both sides with the lateral angles of the head vesicle, 3. the apical plate, a median belt of cells extending from the head vesicle anteriorly to the prototroch. These structures surround two bilaterally situated areas of small ectoderm cells, called "Scheitelplatten" by German authors and designated by Holmes as "rudiments of the cerebral ganglia and eyes"; for the sake of brevity, I will call them "cerebral plates". For further details concerning these structures and their derivation, I may refer to the papers of Rabl (1879), Holmes (1900) and Wierzejski (1905).

2. Structure of the cells (fig. 12). In the ectoderm, a great diversity has appeared. Chiefly, 3 kinds of cells can be distinguished.

The small ectoderm cells form a columnar epithelium of prismatic cells. The nuclei are small, round or slightly elongated, and possess one nucleolus, often with distinct internum. The cytoplasm contains small and rather sparse albumen vacuoles.

The large cells of the head vesicle and velum are rather extended cells with a large, clear, vesicular nucleus, containing one large nucleolus, mostly with distinct internum. In the velar cells, the nuclei have a fine chromatin network; the cells of the head vesicle possess very hyaline nuclei containing only sporadic chromatin granules. In the cytoplasm, numerous albumen vacuoles are found; in the head vesicle cells, they are rather big, whereas the velum cells have smaller albumen vacuoles. Furthermore, vacuolar spaces of irregular shape are found in the head vesicle cells, probably with watery contents. Finally, in the endoplasm, occupying a small inner part of these cells, rather fine γ-granules are present. Several of these cells bear distinct cilia of moderate length, covering the entire outer surface of the cell.

In the apical plate, a third category of ectodermal cells is found. They differ from the former in being less flat, prismatic or conical in shape. The nucleus is big, oval, less hyaline; in the nucleoli no internum has been observed. Most characteristic, however, are the albumen vacuoles. They are numerous and rather large, filling the external part of the cells; their contents is not homogeneous, but consists of irregular morsels and rodlike pieces of coagulum.

The thickened ringlets, described in the preceding chapters, are still present. In one case, 36 of these ringlets were counted; 25 of them were situated in the region of the head vesicle and apical plate; the other in 3 small groups along the posterior median line between the head vesicle and the mouth. Of the cells of the head vesicle and apical plate, nearly all possessed at least one of these ringlets; in a few instances, 2-3 ringlets were present on one cell.

The cells of the entoderm have a large oval nucleus, containing one nucleolus with distinct internum. In the ectoplasmic part of the cell, bounding the archenteron lumen, many spherical albumen vacuoles are present; a much larger vacuole, of irregular outline, lies adjacent to the nucleus, at the side turned towards the archenteron lumen. Evidently, the albumen ingested by the cells undergoes some chemical transformation, as is indicated by its staining reactions: In iron haematoxylin-eosin preparations, the albumen in the archenteron lumen is red, the smaller vacuoles are black, and the big vacuoles light pink; in azan preparations, the colour changes from deep blue in the archenteron, over sky blue in the smaller vacuoles, to nearly colourless in the large albumen vacuole. In the latter, the albumen has sometimes coagulated in the form of pseudo-crystals. Moreover, in the albumen filling the archenteron lumen small vesicular droplets are found, probably representing secretion products of the entoderm cells (cf. above p. 378). As a matter of fact, in some sections the extrusion of droplets from the cells into the lumen has been observed. It is evident, therefore, that an extracellular digestion of the albumen precedes its resorption by the cells. The endoplasmic part of the cells contains many rather fine γ-granules; their size has considerably diminished in comparison to the preceding stage.

The region of transition between ectoderm and entoderm at the mouth is characterized by a special kind of cells, containing rather small oval nuclei with, as a rule, 2 small nucleoli. The cytoplasm is dense and contains some albumen vacuoles of moderate size.

Finally, the mesodermal cells, of different size, are still characterized by their dense protoplasm with many γ-granules, being much smaller than at the preceding stage. The nuclei possess one nucleolus with distinct internum.

3. Mitochondria. In Altmann preparations, small carmine red mitochondria are found especially in the ectoplasmic zone of the ectoderm cells of all types. Likewise, in the entoderm cells the mitochondria are restricted to the ectoplasmic portions bordering the archenteron lumen, where they are especially accumulated around the albumen vacuoles. In the mesoderm, the mitochondria are sparse or lacking altogether. Hence, their distribution has remained the same as at former stages.

4. Cytochemical reactions. a) Fat: In embryos, stained in toto with Scharlach R, the ectoderm is very poor in fat droplets. The entoderm contains, probably, more fat. Most heavily stained, however, are the mesodermal bands.

b) Glycogen: With the iodine reaction, only the glycogen contents of the ectoderm can be estimated. Evidently, it is somewhat greater in the large cells of the head vesicle than in the small ectoderm cells. This is confirmed by sections treated after Bauer. The big cells contain very much glycogen; the small ectodermal cells somewhat less. The cells of the mesoderm contain a moderate quantity of glycogen; the entoderm cells have a narrow layer of glycogen granules along the archenteron lumen, the rest of the cell being poor in glycogen. A distinct boundary exists between these cells and those of the stomodaeum, which resemble the small ectodermal cells.

c) SH-compounds: With fresh eggs, the reaction with alkaline sodium nitroprussiate was positive both in the ectoderm and the entoderm; in the latter, the vacuoles remained colourless. After a prolonged treatment with trichloracetic acid, the reaction was most intense in the entoderm, weaker in the ectoderm. Hence, the whole egg contains both free glutathione and bound sulfhydril compounds, the latter being especially accumulated in the entoderm.

d) Phenolases: With the M-nadi oxidase reaction, an elective blue colouration of the velum, to a lesser extent also of the head vesicle, was obtained; the remaining part of the ectoderm stains less heavily. With high magnification, indophenol blue granules of different size were observed; their density is very great in the large ectoderm cells, much less in the small cells.

e) Peroxidases: The reaction with benzidine and H_2O_2 showed a clearly differential distribution of peroxidases: Two pairs of cells, situated at the lateral angles of the embryo, at the transition between the velum and the head vesicle, stain immediately and intensely; afterwards the rest of the velum and the head vesicle are stained less heavily. With high power, distinct blue granules can be seen; moreover, in all cells the nucleoli are heavily stained.

5. Vital staining. a) Neutral red: In a solution of neutral red, a clearly differential staining occurs. Most heavily stained are the large cells of the apical plate and the anterior cells of the head vesicle, forming a characteristic symmetric figure upon the egg; somewhat less intense is the staining of the velum and the remaining part of the head vesicle, whereas the small ectoderm cells of the other regions are only weakly coloured. The staining of the cells is not diffuse, but granular, the size of the stained patches differing in different regions. When the embryos are flattened under a coverslip, and observed with oil immersion, the relations become clear. The stain is bound to neutral red vacuoles in the ectoplasm of the cells. In the large cells of the head vesicle, numerous large neutral red vacuoles are present. In the cells of the apical plate, these vacuoles are equally large, but contain distinct pseudocrystals of albumen. In the velum cells, the vacuoles are numerous, but much smaller. The small ectoderm cells have only sparse small vacuoles. In the entoderm cells, only one or a few very large neutral red vacuoles are present; they contain pseudocrystals of albumen, and are clearly identical to the albumen vacuoles. Finally, cells wholly without neutral red vacuoles are found, representing, probably, the mesoderm cells.

From these observations, one thing becomes very clear: The neutral red vacuoles do not only correspond in their size and position entirely to the albumen vacuoles, but both structures are doubtless identical. Hence, the neutral red is accumulated in the albumen vacuoles.

The question arises whether this accumulation of neutral red is due to the properties of the living protoplasm, or is a passive absorption of the dye by the albumen in the vacuoles. In this connection it is interesting to note that the egg capsule fluid is only very weakly stained, even after a prolonged stay of the egg capsules in a rather concentrated dye solution. Though it is possible that the albumen in the vacuoles is concentrated or altered in such a way that its staining properties have increased, it seems more likely that the accumulation of the neutral red in the vacuoles is due to a special activity of the vacuole walls.

b) In nile blue hydrochloride and brilliant cresyl violet, an elective absorption of the dye in the cells of the head vesicle and apical plate, to a less extent also in the velum cells, occurs. The small ectoderm cells are only weakly coloured. Nile blue hydrochloride stains the yolk granules green, the albumen vacuoles deep blue, while fine granules in the cytoplasm, probably mitochondria, are stained heavily. Brilliant cresyl violet gives a diffuse staining of the cytoplasm and causes the formation of dark violet granules in the albumen vacuoles.

c) With methylene blue and Janusgreen, the results are similar as at previous stages. Intact cells do not stain. When the embryos are placed in a weak, acidified Janusgreen solution in tap water, the ciliary movement stops immediately.

6. Summary. The beginning of differentiation in the ectoderm characterizes this stage. A clear distinction has appeared between the big, flat, extended cells of the head vesicle, apical plate and velum, and the small, columnar cells covering the rest of the embryo. The former have more numerous and larger albumen vacuoles, more glycogen, a greater amount of peroxidases and phenolases, and show a stronger absorption of basic dyes, which are accumulated in the albumen vacuoles.

As a matter of fact, the large ectodermal cells are not identical in all regions; they show small, but regular differences. The albumen vacuoles are smaller in the velum cells, large in the cells of the head vesicle and apical plate; in the latter, their contents has a crumbled appearance, and consists of pseudocrystals of albumen. The absorption of basic dyes is maximal in the apical plate and the foremost cells of the head vesicle; in the latter, also the glycogen reaction reaches its highest intensity. The velum cells contain the greatest amount of phenolases, while the peroxidases are especially abundant in 2 cells at the transition between velum and head vesicle. Hence, a definite pattern of differentiation has appeared in the ectoderm.

In the entoderm, no clear distinction between different kinds of cells has as yet appeared. The albumen vacuoles in the immediate vicinity of the nucleus have grown to large dimensions. Definite symptoms of a digestion of the albumen, both extra- and intracellular, can be observed. The cells contain a moderate amount of fat and of bound SH-compounds.

The cells of the stomodaeal region have special properties, the regular occurrence of two nucleoli in each nucleus being most characteristic.

Finally, in the mesoderm cells no great changes as compared to the previous stage have occurred.The γ-granules have decreased in size. The cells contain a great abundance of fat droplets, but hardly any mitochondria.

V. Further differentiation

1. External appearance. In this chapter, two further stages are studied: early trochophore and late trochophore stage. At the early trochophore stage, the embryo begins to increase considerably in size; this growth is partly due to the swelling of the head vesicle, partly to the increase in size of the albumen cells of the entoderm. The velum has become more conspicuous. The mouth has been reduced to a narrow slit. At the posterior side, the shell gland rudiment has become visible in the form of a shallow groove. In the entoderm, a clear distinction between small columnar epithelial cells and large albumen cells has appeared; the latter begin to swell considerably by an augmented ingestion of albumen. The rudiment of the hind gut forms a solid cell mass against the posterior side of the mid gut.

At the late trochophore stage, the growth of the embryo has continued; at the same time, it has become very transparent, the albumen cells of the gut shining through the ectoderm like a bunch of grapes filling a large part of the embryo. The velum and head vesicle are still well developed, but the area encircled by them occupies a smaller part of the surface of the embryo, in consequence of a relatively faster growth of the ventral regions. The foot anlage is beginning to protrude. The shell gland forms a deep invagination; the formation of the shell has begun. The mouth has become wider again, and leads into a wide mouth cavity, which bears ventrally the rudiment of the radular sac; a short oesophagus, the lumen of which has, however, been obliterated, connects it with the gut. The albumen cells of the gut have grown still larger. In the hind gut, a lumen has appeared, which has, however, no communication with that of the mid gut. At both sides, the protonephridium is well developed; it opens to the exterior immediately below the velum.

For further details, the reader is referred to the papers of Rabl, Holmes and Wierzejski mentioned above, and to the paper of Bloch (1938).

2. Structure of the cells. At the early trochophore stage, the small ectodermal cells are prismatic in shape (fig. 13a). They have a small spherical or oval nucleus, containing 1-2 nucleoli without internum. The ectoplasm is dense, the endoplasm contains granules. These granules differ in some respects from the γ-granules of previous stages; e.g., after staining with azan, they are not orange, as the latter, but have a bronze green tint. I will call them δ-granules. At the late trochophore stage, the number of these granules has considerably decreased.

The cells of the shell gland rudiment do not differ much, at the early trochophore stage, from those described above; only, their ectoplasm is still more dense. At the late trochophore stage, however, a considerable change has occurred. The cells have grown to long prisms; the δ-granules have disappeared; the outer part of the cells contains a filamentous secretion product, which is continued into a similar substance filling the lumen of the invagination.

At the early trochophore stage, among the large ectodermal cells 3 categories can be distinguished. The first consists of rather flattened cells, with a large oval nucleus, containing a spherical nucleolus with distinct internum, and a fine chromatin network. Their surface bears a continuous layer of rather short cilia. The cytoplasm consists of 3 layers: The outer zone is very dense and contains numerous fine granules; the middle layer has many albumen vacuoles of moderate size; while the basal zone of the cell contains a dense mass of δ-granules (fig. 13b). This cell type is especially characteristic of the head vesicle.

The second type differs from the preceding mainly by the greater dimensions of the albumen vacuoles in the middle zone of the cytoplasm, their average diameter being about twice as large. These cells form the apical plate and the major part of the velum.

The latter consists, at this stage, anteriorly of a single row of cells only, having the characteristics just described. Posteriorly, however, a second row appears above the former, consisting of two cells of special type. In the main, they resemble the other ciliarly cells; the outer zone of the cytoplasm contains many fine granules having the characteristics of the α-granules of early stages; the middle zone has numerous small albumen vacuoles; the basal layer possesses δ-granules. What distinguishes these cells from the other ciliary cells is especially the composition of the nucleolus. In all other cells of the embryo, the nucleoli show the same staining reactions; in iron haematoxylin-eosin preparations, they are black; in sections stained with azan, they have a deep red color. In the 2 pairs of cells just mentioned, however, the nucleolus stains, at least partly, red with iron haematoxylin-eosin, whereas in azan preparations it is violet blue. This different staining reaction, which is very conspicuous at this stage, points to a peculiar physicochemical composition of the nucleolus of these cells.

A comparison with the figures of HOLMES (1900) and WIERZEJSKI (1905) makes it likely that these cells are the descendants of the anterior trochoblasts. Considering their position in the embryo, it may be supposed that they correspond to the cells showing an extreme abundance of peroxidases already at the previous stage, especially in view of the observed localization of these substances in the nucleoli; this could, however, not be proved with certainty.

At the late trochophore stage, the large ectodermal cells have flattened considerably, especially in the head vesicle and apical plate. In consequence of this, their structure is less clearly visible. Albumen vacuoles of moderate size and δ-granules are still present in the cells of the head vesicle. In the velum, the cells of the inferior row contain a dense mass of granules, but hardly any albumen vacuoles.

The peculiar ringlets, present in previous stages on the surface of many ectodermal cells, have been greatly reduced. At the early trochophore stage, a few of these ringlets are still found; in the late trochophore, they seem to have disappeared altogether.

The gut communicates, at the early trochophore stage, with the outer world by means of a narrow slit-like stomodaeal canal. The outer 1/3 part of this canal is formed by prismatic cells, having the appearance of small ectoderm cells, but charac-

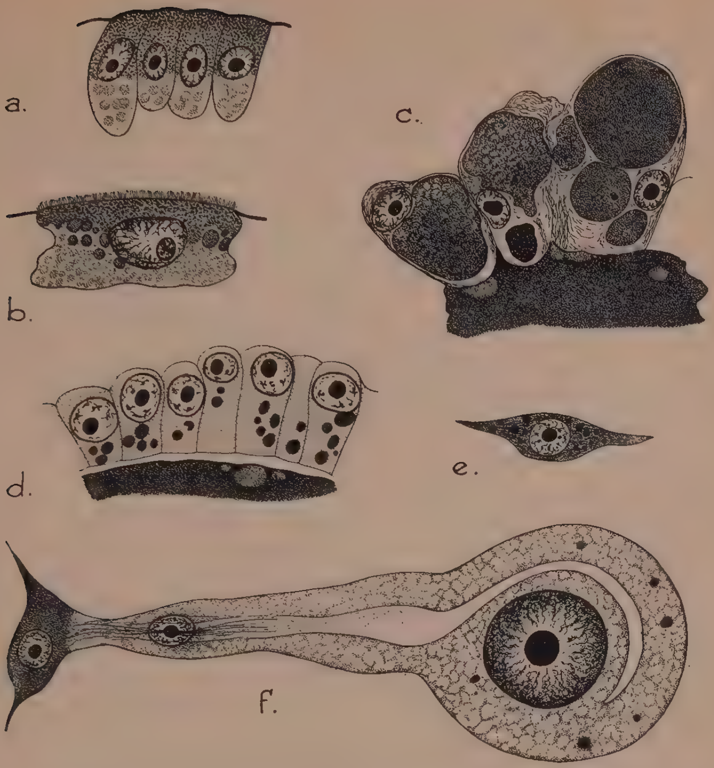

Fig. 13. Trochophore stage of *Limnaea stagnalis*. a. Small ectoderm cells. b. Ectodermal ciliary cell. c. Albumen cells of gut. d. Small entoderm cells of gut epithelium. e. Mesenchyme cell. f. Protonephridium (without aperture cell).

terized by the presence of an especially dense ectoplasm. The inner 2/3 are bordered by more cubic cells, with lighter protoplasm and less δ-granules.

At the late trochophore stage, considerable changes have taken place in this region. The outer part of the stomodaeal canal has given rise to a wide mouth cavity, bordered by an epithelial wall of high prismatic cells with oval nuclei; the outer zone of the cells is formed by a dense ectoplasm; δ-granules are absent. At the ventral side, the radular sac has appeared as a spherical outgrowth of the mouth cavity; its cells are wedge-shaped and have a clear protoplasm. The mouth cavity is connected with the mid gut by a short oesophagus with obliterated lumen; it consists of very clear cells with a vacuolated protoplasm, having the appearance of turgor cells.

In the entoderm, a clear distinction between small epithelium cells and large albumen cells has appeared at the early trochophore stage. As for their relative positions, I may refer to the paper of Bloch (1938).

The albumen cells have reached considerable dimensions (fig. 13c). They are filled with albumen vacuoles of different size; in the basal part of the cell, there are one or a few huge vacuoles of irregular shape, whereas the apical part (directed towards the lumen of the gut) contains several smaller vacuoles, which are, as a rule, nearly spherical. Both kinds of vacuoles differ somewhat in their staining reactions; in iron haematoxylin-eosin preparations, the contents of the smaller vacuoles is black (like the albumen coagulum in the lumen of the gut), whereas the albumen in the large vacuoles is, chiefly, red, but may contain black irregular masses or pseudocrystals in its centre (the latter are also visible in embryos stained in vivo with neutral red, and are, therefore, no mere coagulation products). With other staining methods, similar differences have been observed; they show that the albumen, at least in the huge basal vacuoles, undergoes some chemical change. That the digestion of the albumen is, in part, extracellular, is indicated by the fact that the coagulum in the gut often shows clear crescent-shaped areas at its zone of contact with the cells of the wall, suggesting a secretion of digestive juices by the latter.

The nuclei of the albumen cells are large, oval or irregularly compressed; they contain a large nucleolus without internum. Their position differs; often, they lie in the middle region of the cell, between the large and smaller vacuoles, but they may also be situated at the basal end of the cell, or sideways. The cytoplasm contains many ∂-granules, especially in the basal part; at the late trochophore stage, however, these granules have disappeared nearly altogether.

The small entoderm cells are prismatic and form a regular epithelium. At the early trochophore stage, the nucleus lies in the basal part of the cell; it is spherical or oval, and has one nucleolus without internum. The greater apical part of the cell is occupied by many small albumen vacuoles (fig. 13d). These have disappeared at the late trochophore stage; the nuclei have returned to the middle of the cells.

The hind gut rudiment consists at the early trochophore stage of a solid group of cells, with round or slightly elongated nuclei, often possessing 2 or more small nucleoli; in the cytoplasm, sporadic ∂-granules are present. In the late trochophore, the rudiment has enlarged considerably, and has got an elongated shape. A narrow lumen has formed, around which the cells have arranged themselves radially. The nearly spherical nuclei, situated in the basal part of the cells, have mostly one nucleolus. The ∂-granules have disappeared.

The mesoderm has developed into a mesenchyme, occupying the space between ectoderm and entoderm, and forming an investment around the organs arising from these layers. Its cells are spindle-shaped, the spherical or elongated nucleus has one nucleolus without internum. In the cytoplasm, many ∂-granules are present (fig. 13e).

At both sides of the body, 4 mesodermal cells have developed into a protonephridium. At the early trochophore stage, it has not yet fully differentiated. Most conspicuous is the giant excretory cell, situated beneath the ectoderm at the level of the lateral edges of the velum. Its large vesicular nucleus is bigger than any other of the body; it contains a huge nucleolus, with an internum often consisting of several droplets of different size. The chromatin is mainly agglomerated in a peripheral network beneath the nuclear membrane. The cytoplasm contains many ∂-granules, and an intracellular nephric channel, opening to the outside with a pore below the velum. This channel curves round the nucleus of the giant cell, and is continued by a prolongation in the bodies of 2 smaller cells, sitting on the top of the giant cell.

At the late trochophore stage, the last-mentioned cells have differentiated into a terminal cell, possessing a dense cytoplasm intruding with many prolongations between the neighbouring mesenchyme cells, and projecting with a tuft of long cilia into the lumen of the nephric channel; and a perforated canalicular cell; both have a spherical or oval nucleus with one nucleolus (fig. 13f). The giant excretory cell has still increased in size; its cytoplasm is rather clear and lightly stained, the nucleus shows the same characteristics as before. Finally, the aperture cell, situated at a level with the ectoderm, is not very conspicuous; it has a spherical nucleus with a nucleolus without internum.

3. Golgi bodies and mitochondria. The Golgi bodies have been studied in an embryo with well developed shell rudiment, one day after the late trochophore stage. In the ectodermal cells, sporadic Golgi systems are present either in the ectoplasm or the endoplasm; their shape and localization vary in different regions of the body. The ciliated cells of the velum contain numerous Golgi systems of varying size all through the cytoplasm; the outer zone of the cell is strongly osmiophilic. In the shell gland area, especially the marginal cells, being most active in the formation of the shell, possess a markedly osmiophilic ectoplasm; in the central cells of the field irregular networks of Golgi substance are present. Both the cells of the stomodaeum and those of the radular sac have numerous Golgi systems in the ectoplasm; in the stomodaeum they are, as a rule, spherical in shape, in the radular sac more elongated or rod-shaped. The albumen cells of the gut contain Golgi systems, especially in the basal parts of the cells; the small entoderm cells have Golgi systems of irregular shape only in the ectoplasmic part. The mesenchyme cells and muscle cells contain osmiophilic granules and filaments; the cytoplasm of the giant excretory cell of the protonephridium is strongly osmiophilic throughout. The cells of the definite kidney contain Golgi systems in their inner zone, being mostly elongated and forming peculiar loops.

In general, these observations agree with those recorded by HIRSCHLER (1918). Small disparities may partly be due to differences in technics, partly to a different age of the embryos studied. The observations show that in various tissues of the body Golgi systems, of different shape and intracellular localization, have developed, indicating an increased metabolic activity of the cells.

In Altmann preparations of the same stage, the outer zone of the large ectodermal ciliary cells of the skin and in the stomodaeum shows an intense diffuse red colouration; in the rest of the cell, numerous rather large red granules are present. In the albumen cells of the gut, the cytoplasm is filled with innumerable small carmine red mitochondria. In the giant cell of the protonephridium, numerous rather large red granules are found. The other tissues (small ectoderm cells, small entoderm cells, mesenchyme) contain only sporadic mitochondria. Iron haematoxylin preparations show the same localization of mitochondrial substances.

At a somewhat later stage, similar results were obtained. Large ectodermal ciliary cells are found in the velum, head vesicle, in the median line of the foot; furthermore, a narrow dorsomedian ciliary band is present in the stomodaeum, a broader ventromedian area in the oesophagus. In all these places, the cells show the same characteristics: The outer zone of the cytoplasm stains intensely both in Altmann and in iron haematoxylin preparations; the rest of the cell contains rather large mitochondrial granules. Moreover, in the ectoderm of head and foot scattered small ciliary cells have differentiated; they show the same characteristics. The protonephridia contain distinct mitochondrial granules. Finally, numerous mitochondria are found in the cytoplasm of the albumen cells of the gut. The other tissues of the body contain hardly any mitochondrial substances.

4. Cytochemical reactions. a) Fat: In embryos of the late trochophore stage, fixed in formol and stained with Scharlach R, the localization of fat droplets has been studied. The fat is especially accumulated in the mesoderm. The giant cell of the protonephridium is heavily stained; with high magnification, innumerable fat droplets are seen in the cytoplasm. In the albumen cells of the gut, numerous fat droplets are visible in the walls between the vacuoles, especially in the triangular interstices where 3 cells meet. The ectoderm contains only sporadic fat droplets. At a somewhat later stage, however, it was observed that the cells of the velum contain a moderate amount of fat droplets, contrary to the rest of the ectoderm, which is very poor in fat.

b) Glycogen: At the early trochophore stage, with the iodine reaction a distinct elective reddish brown colouration of the large ectodermal ciliary cells was observed. It was most intense in the head vesicle, somewhat less in the apical plate and velum, while a weak colouration of the circumference of the mouth and the median line of the foot was indicated. Similar results have been obtained at the late trochophore stage.

At a still somewhat older stage, the distribution of glycogen was studied in sectioned embryos with Best's carmine. In the large ciliary cells of the ectoderm, the cytoplasm, with the exception of its outermost zone, is full of large glycogen granules. Furthermore, a large amount of glycogen is present in the protonephridium. In the terminal and canalicular cells, it is accumulated in the neighbourhood of the nuclei; in the giant cell, however, large glycogen granules are found throughout the cytoplasm. It could not be determined, whether the albumen cells of the gut contain glycogen, in consequence of the strong affinity of the albumen in the vacuoles for the stain; in control preparations, treated with saliva, the glycogen granules in the ciliary cells and protonephridium have disappeared, but the albumen cells show the same picture. Likewise, in the other tissues of the body no glycogen could be determined with any degree of certainty. It is possible, however, that small amounts of the substance may have escaped observation in consequence of the fact that the mucoids are heavily stained with Best's carmine, which thwarts the analysis.

c) Thymonucleic acid: At the early trochophore stage, Feulgen preparations show a considerable augmentation of thymonucleic acid, as compared with previous stages. Nearly all resting nuclei possess distinctly stained chromatin particles. The nucleoli are colourless, but in some cases they are surrounded by a crowd of small granules rich in thymonucleic acid. Interesting differences in amount of thymonucleic acid between the tissues exist. The resting nuclei of the small ectoderm cells, shell gland, albumen cells and giant cell of the protonephridium are very rich in thymonucleic acid; those of the mesenchyme cells contain less of this acid; while the large ciliary cells of the ectoderm have nuclei containing hardly any thymonucleic acid at all, being nearly colourless in Feulgen preparations.

At the late trochophore stage, the resting nuclei of the small ectoderm cells, shell gland, stomodaeum, radular sac, small entoderm cells, albumen cells of the gut, and hind gut are still rather rich in thymonucleic acid; those of the ectodermal ciliary cells show the same reaction as before, remaining very pale in Feulgen preparations. An interesting change has taken place in the nuclei of the giant excretory cells; they have lost most of the thymonucleic acid they contained, and are very pale at this stage.

d) Ribonucleic acid: The distribution of ribonucleic acids was studied at the late trochophore stage after BRACHET; interesting results have been obtained. The total amount of these acids differs very much in different tissues of the embryo. The small ectoderm cells, shell gland, stomodaeum and radular sac, small entoderm cells, hind gut and mesenchyme cells are very rich in ribonucleic acids; their amount is only small in the albumen cells of the gut and the protonephridium; while the large

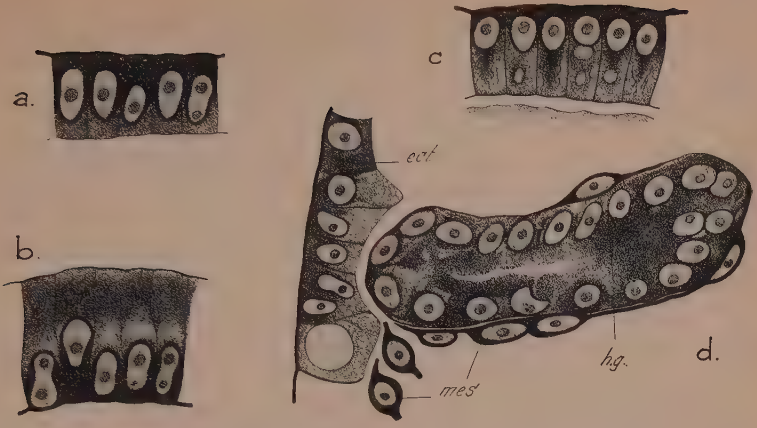

Fig. 14. Trochophore stage. Distribution of ribonucleic acids in a. small ectoderm cells; b. shell gland; c. small entoderm cells; d. hind gut (*h.g.*), mesenchyme cells (*mes.*) and ectoderm (*ect.*).

ectodermal ciliary cells and the oesophagus are practically devoid of ribonucleic acid. Furthermore, there are significant differences in their intracellular localization. In the small ectoderm cells of the skin, these substances are especially accumulated in the outer part of the cells and around the nuclear membranes (fig. 14a, d); the nucleoli of these cells seem to contain very little ribonucleic acids: they stain moderately in Unna preparations, but show the same picture in controls treated with ribonuclease. In the shell gland, the ribonucleic acids are especially concentrated in the basal part of the cells; a second zone, of much less intensity, lies about half way between the nucleus and the outer surface (fig. 14b); the nucleolus and nuclear membrane both contain the acids. In the stomodaeum, the outer part of the cells shows the greatest concentration of ribonucleic acid, whereas in the radular sac the "nuclear membrane nucleotides" (HYDEN 1943) are strongly developed. In the small entoderm cells of the gut epithelium, the major accumulation of these substances is situated basally and around the nuclear membrane (fig. 14c); the nucleoli contain a moderate amount, while the apical part of the cells has only little ribonucleic acid. In the hind gut, especially the nuclear membrane nucleotides are very conspicuous (fig. 14d). The albumen cells show a uniform, but rather low concentration of ribonucleic acids throughout their cytoplasm; the nuclear membrane is heavily stained. The mesenchyme cells have a high concentration of this substance in their cytoplasm, especially in the neighbourhood of the nuclear membrane (fig. 14d). Finally, in the protonephridium the concentration is rather low; most ribonucleic acid is found in the cytoplasm of the terminal cell and around the nuclei of the canalicular and giant cells; the nucleoli, which are heavily stained in Unna preparations (except the internal droplets), are equally dark in ribonuclease controls, and seem, therefore, not to contain the acids.

e) SH-compounds: At the late trochophore stage, the reaction with alkaline sodium nitroprussiate furnished the following results: Fresh eggs gave a strong reaction of the ectoderm, much less or hardly at all in the entoderm. After treatment with trichloracetic acid, the reaction was maximal in the mesoderm and entoderm, less intense in the ectoderm. Hence, free glutathione is found predominantly in the ectoderm, bound SH-compounds especially in the inner layers (cf. Lison 1936).

At a still later stage, the free glutathione is found especially in the ectoderm of head and foot, to a less extent also in the mantle fold, whereas the bound sulfhydril-compounds are present in the gut epithelium (but not in the albumen cells) and the ectoderm, especially of the head region.

f) Phenolases: With the M-nadi oxidase reaction, both at the early and the late trochophore stage the whole ectoderm shows a rather equal colouration by indophenol blue granules of variable size; the entoderm stains more slowly. The circumference of the mouth and the velum, at the older stage also the shell gland, show a somewhat stronger reaction, but the difference is slight. At still older stages, however, an extremely strong reaction of the shell is observed, increasing with further development; moreover, a somewhat less intense reaction of the mantle fold, encircling the outer border of the shell, occurs. Finally, scattered subepidermal cells are crowded with deep blue granules of indophenol blue. In the ectoderm, sporadic granules appear; their density is somewhat greater in the cells of the velum. In the head and foot, a diffuse violet colour appears, indicating a secondary adsorption of the formed indophenol blue at the cell lipoids.

g) Peroxidases: The benzidine peroxidase reaction at the late trochophore stage gave the following interesting results: A rapid and intense blue colouration occurred at 3 points, viz., the lateral angles of the velum, and a small pit at the ventral side of the intestinal sac, ventrally to the shell gland. Weaker was the reaction in the entodermal gut, still weaker in the ciliary cells of the rest of the velum, the apical plate and head vesicle, the median line of the foot and around the mouth. The remaining part of the embryo was practically colourless.

At still later stages, an elective very strong reaction appears in the mantle fold. In the shell, the reaction begins very soon (in fact, often the first blue colouration is observed in this region), but remains rather weak, contrary to the phenolase reaction. Moreover, scattered cells in the interior of the embryo become deep blue; especially their nucleolus is heavily stained. Whether these cells are identical to those stained in the M-nadi oxidase reaction is difficult to decide; I got the impression, however, that they belonged mostly to deeper layers of the mesenchyme, immediately surrounding the albumen cells of the gut.

h) Iron: At the early trochophore stage, the large ectodermal cells and the giant excretory cells of the protonephridium show the largest concentration of free iron. The entoderm contains somewhat less, the small ectodermal cells still less iron. The nucleoplasm is free of iron, but the nucleoli show a distinct blue colour with the Prussian blue reaction.

In the late trochophore, this differential distribution has become more conspicuous. The concentration of free iron is greatest in the large ciliated ectoderm cells and the protonephridium, somewhat less in the stomodaeum and the entoderm, still less in the small ectoderm cells, where the iron granules are accumulated in the basal parts of the cells.

At still later stages, the differences in iron distribution increase still more. In a late "veliger" stage (8 days old), only the protonephridia and the large ciliary cells of the velum and head vesicle, around the mouth, in the pharynx and the oesophagus contain a large quantity of iron granules, in the albumen cells of the gut some scattered groups of iron granules are still present, the other tissues have become free of iron. In a 10-day embryo, only the ciliary cells contain iron granules; in the next days, they disappear gradually. The last traces of free iron are found in a 12-day embryo in some cells of the neck region (remains of the head vesicle). At hatching, no free iron can be detected any more (Miss E. Exalto, unpublished).

5. Vital staining. a) Neutral red: At the early trocho-

phore stage, in the ectoderm an elective colouration of the velum, apical plate and anterior cells of the head vesicle takes place. In the entoderm, the albumen cells are distinctly stained. The neutral red is accumulated in the albumen vacuoles of the cells.

At the late trochophore stage, an interesting phenomenon makes its appearance. The albumen cells of the gut are heavily stained in a deep carmine red tint, whereas the ectoderm, especially the large ciliary cells, get a rust brown colouration. In both, the neutral red is bound to the albumen vacuoles, but the tint of these vacuoles is extremely different in ectoderm and entoderm. This points to the existence of a different pH in the albumen vacuoles of both tissues at this stage of development.

At a still later stage (embryo 2 days older), this difference in reaction has still been accentuated; the deep carmine red albumen cells shine through a brownish yellow ectoderm. The velum stains heavily in the same tint as the other ectoderm.

b) Nile blue hydrochloride: At the early trochophore stage, the large ectodermal ciliary cells are heavily stained. As in previous stages, the dye is bound to the yolk granules, albumen vacuoles and mitochondria. In the velum cells the green tint of the yolk granules predominates, whereas the apical plate has a blue colour by the presence of large deeply stained albumen vacuoles. The albumen cells of the entoderm have distinctly blue albumen vacuoles.

At later stages, a difference in colour between ectoderm and entoderm appears: The entodermal albumen cells are deep azure blue, whereas the ectoderm (especially the velum) has a more violet blue tint.

c) Brilliant cresyl violet: At the late trochophore stage, the ectoderm stains diffusely violet. An elective staining, in a red tint, of the large ciliary cells of the velum, apical plate, border of the mouth and median line of the foot, is very obvious. The entoderm does not stain.

d) Cresylechtviolet: Older embryos (with well developed shell and mantle fold), stained with cresylechtviolet, showed an interesting difference in staining reaction between ectoderm and entoderm. The ectoderm has got a pink colour, the velum being electively stained in the same tint; the albumen cells of the gut, on the contrary, have become light blue. This colour difference, corroborating those observed in neutral red and nile blue hydrochloride, indicates that the pH in the ectoderm cells (especially in their albumen vacuoles) is higher than that in the albumen cells of the gut.

e) Methylene blue: As at previous stages, the living cells remain colourless in this dye. At the late trochophore stage, only the first rudiment of the shell is stained.

f) Janusgreen does not stain, neither the early nor the late trochophores.

6. Summary. At these stages, the differentiation progresses rapidly. In all germ layers, cells of different composition, both morphologically and chemically, have developed.

In the ectoderm, the major contradistinction is that between the small ectoderm cells of the skin, with nuclei rich in thymonucleic acid, but a nucleolus without ribonucleic acid, with cytoplasm rich in ribonucleic acid and glutathione, but poor in Golgi systems, mitochondria, fat and glycogen, on one hand; and large ciliated cells, with nuclei poor in thymonucleic acid, cytoplasm without ribonucleic acids, but rich in Golgi systems, mitochondria and glycogen, and with more fat droplets than the small ectoderm cells, on the other.

Among both kinds of cells, minor differences exist. In the area of small ectoderm cells, it is especially the shell gland region that shows particular characteristics. At the time when the shell is being formed, this region is characterized by a considerable accumulation of phenolases and peroxidases. The latter have their greatest concentration in the outer border of the shell region (mantle fold), where the cells are most active; these cells contain also a large amount of phenolases and have a strongly osmiophilic ectoplasm. The phenolases are most concentrated in the shell itself, which contains, moreover, a moderate amount of peroxidases.

The large ciliated cells have a cytoplasm consisting of 3 zones; the outer part contains a large amount of diffuse mitochondrial lipoids; the middle zone of albumen vacuoles and the basal zone of δ-granules are both characterized by the presence of numerous Golgi systems, mitochondria and a large quantity of glycogen. The albumen vacuoles of the middle zone, which show an alkaline reaction, have a strong affinity towards neutral red and nile blue hydrochloride. Thus, these cells show a great resemblance, in their structure and chemical composition, with the velum cells of Nudibranchs studied by CARTER (1928).

As for regional differences among the ciliated cells, we may recall, apart from the differences in size of albumen vacuoles, the following points: The anterior cells of the head vesicle contain very much glycogen, and have a strong affinity towards basic vital dyes. The velum cells contain less glycogen, but have, especially at later stages, a moderate amount of fat droplets. Two pairs of cells at the transition between velum and head vesicle, probably the descendants of the anterior trochoblasts, are characterized, outer by the aberrant staining reaction of their nucleoli, by an extremely large amount of peroxidases; as the latter seem to be localized, to a large extent, in the nucleoli, both phenomena are, presumably, linked.

In the stomodaeal region, the cells of the mouth cavity and radular sac resemble the small ectoderm cells in most respects; those of the oesophagus, on the contrary, are characterized by their highly vacuolated protoplasm, containing only very little ribonucleic acid.

In the entoderm, two kinds of cells have developed: small entodermal cells of the gut epithelium, and large albumen cells. In the former, the albumen vacuoles of previous stages become smaller, finally to disappear entirely; in the latter, they increase enormously in size, and an active digestion of albumen, both extra- and intracellular, has begun. Of other differences, the following may be enumerated: The small entoderm cells contain a large amount of ribonucleic acids and of sulfhydril compounds bound to proteids. The albumen cells contain less ribonucleic acids and sulfhydril compounds, but many mitochondria and fat droplets.

As for the mesoderm, it is interesting to compare the mesenchyme on one side, the protonephridia on the other. The mesenchyme cells have nuclei with a moderate amount of thymonucleic acid; their cytoplasm is rather rich in fat and osmiophilic substances, and contains a large amount of ribonucleic acids. At later stages, particular subepidermal cells, extremely rich in phenolases, and other cells, containing a great abundance of peroxidases, develop. The cells of the protonephridium (especially the giant cell) are characterized by nuclei, being at first rich, but later poor in thymonucleic acid, having nucleoli with well developed complex internum, which do not contain ribonucleic acids. The cytoplasm is osmiophilic and contains numerous mitochondria and fat droplets, a large amount of glycogen, but only a small quantity of ribonucleic acids.

DISCUSSION

1. The vitelline membrane and its behaviour during cleavage

The uncleaved egg of *Limnaea* is surrounded by a fine plasmatic lamella, the vitelline membrane. The existence of such a membrane in the Pulmonate egg has been the subject of some controversy; whereas a few authors (e.g. WIERZEJSKI 1905, COMANDON & DE FONBRUNE 1935) did observe it, others (e.g. RABL 1875, FOL 1879, KOFOID 1895) deny its presence in this group. As a matter of fact, in freshly laid eggs the membrane is extremely thin, and so tightly apposed to the egg surface that it is invisible in the living state; only in sectioned eggs its presence can be demonstrated. When the 1st polar body forms, it pierces the vitelline membrane and comes, therefore, to lie outside it. Between both maturation divisions, however, a change in the consistency of the membrane seems to take place; the 2d polar body lifts it, at least partly, from the egg surface; another vitelline membrane lamella remains, however, apposed to the egg surface or is formed anew, so that the 2d polar body comes to lie between the two layers into which the vitelline membrane has been split in this region.

When the 1st cleavage furrow begins to cut through the egg, the vitelline membrane remains apposed to the egg surface, and is, therefore, carried inward with the furrow. At the moment of maximal rounding off of the blastomeres, the advancing margins of the vitelline membrane meet from all sides in the middle and, in this way, both blastomeres are completely surrounded by a vitelline membrane lamella. When, thereafter, the blastomeres flatten against each other with their adjacent sides, the vitelline membrane lamellae covering these sides fuse into a single partition wall separating the blastomeres. Soon, however, they go asunder again in places, forming lenticular spaces which coalesce into a single cleavage cavity. The surfaces of the cells bordering the cleavage cavity (including the "secretion-cones") remain, therefore, covered by a fine lamella which is a derivative of the original vitelline membrane.

At the next cleavages, the behaviour of the vitelline membrane is the same, as far as could be made out. We may conclude, therefore, with some degree of certainty that also at later stages both the cell boundaries and the outer lamellae upon the free surfaces of the cells (turned to the exterior and to the cleavage cavity) can be derived, ultimately, from the original vitelline membrane.

After the kinematographic observations of COMANDON & DE FONBRUNE (1935), the embryo of *Limnaea limosa* leaves its chorion during the 2d day of development, with the beginning of ciliary movement. I have not been able to observe this phenomenon in *Limnaea stagnalis*.

Further information concerning the nature of the vitelline membrane can be gained from the behaviour of *Limnaea* eggs in Ca··-free media (RAVEN & KLOMP, 1946). In such media, e.g. distilled water or solutions of urea and sucrose, the eggs cleave in a peculiar way: the cleavage furrow advances normally till the maximal rounding off of the blastomeres; the process of flattening of the latter, however, stops in its initial phases; the blastomeres remain connected by a narrow stalk only; no cleavage cavity is formed. Furthermore, the vitelline membrane loses its contact with the egg surface in the region of the cleavage furrows; it bridges the furrow from one blastomere to the other. Ultimately (e.g. in sucrose solutions ± 0.08 Mol), the membrane releases itself completely from the egg surface; the blastomeres, which have lost all connection, form a loose heap surrounded by the membrane. Evidently, this abnormal cleavage in Ca··-free solutions is brought about by a change in properties of the vitelline membrane, which at once separates and unites the blastomeres in normal cleavage.

Finally, some observations on the nature of the vitelline membrane have been made in the course of our experiments on the swelling and shrinking of the eggs of *Limnaea* in hypotonic and hypertonic solutions (RAVEN & KLOMP, l.c.). In eggs shrinking in hypertonic urea or sucrose solutions, the vitelline membrane is often thrown into folds. On the other hand, in hypotonic solutions the eggs show a subnormal swelling, which betrays itself by an extremely high value of the calculated "non-solvent volume" (average: 57%; for swelling alone: 68%); this may be due to the resistance the vitelline membrane offers to the swelling of the egg.

It is clear from these observations that the "vitelline membrane" of *Limnaea* is a rather peculiar structure. In its various aspects, it shows points of agreement with different structures in other eggs. Its role in cleavage, as indicated by the influence of Ca··-free media, corresponds to that of the "hyaline membrane" of sea urchins (MOORE 1928, 1930; E. B. HARVEY 1934, 1935); both serve to hold together the blastomeres. Their consistency is, however, quite different, the vitelline membrane of *Limnaea* being a firm, rather inelastic membrane; there are no indications that it can be centrifuged off the egg; furthermore, it is not completely dissolved in Ca··-free media, like the "hyaline membrane" of sea urchins.

In view of its behaviour in normal cleavage, where it grows inward with the cleavage furrows and ultimately forms the cell boundaries and covers all free cell surfaces, the "vitelline membrane" of *Limnaea* is, apparently, a layer of living protoplasm which belongs to the cortical cytoplasm of the egg. Recent observations (SCHECHTMAN 1937; DAN, YANAGITA & SUGIYAMA 1937; DAN, DAN & YANAGITA 1938; CHAMBERS 1938, 1939) have shown that the egg cortex plays an active and predominant role in the cleavage process. The formation of the cleavage furrow must be ascribed to changes in the physical state of a gelated cortical layer showing local phenomena of contraction and expansion. This gelated cortex in sea urchins is covered externally by a protoplasmic surface layer, which preserves the integrity of the underlying protoplasm (CHAMBERS 1939) and equalizes the local differences of tension of the underlying cortical layer (DAN c.s. 1937).

The observation that the cleavage furrow is completed in *Limnaea* in Ca··-free media in spite of the dislocation of the "vitelline membrane" in this region proves that the latter is not the active part of the egg cortex. Apparently, it corresponds, therefore, to the protoplasmic surface layer mentioned above. The gelated cortical layer responsible for cleavage must be sought, probably, in a very thin protoplasmic layer forming the outer boundary of the subcortical protoplasm.

One objection might be made against the identification of the "vitelline membrane" of *Limnaea* with a part of the egg cortex. According to MOTOMURA (1935), in sea urchins in normal cleavage the cell boundary is no derivative of the egg cortex forming the original surface of the cell, but a new formation arising by the gelification of protoplasm at the top of the cleavage furrow. This does not correspond to the behaviour of the "vitelline membrane" of *Limnaea* during cleavage. However, in sea urchins the cleavage furrow in normal cleavage does not completely separate the blastomeres, as in *Limnaea*. Cleavage in *Limnaea* agrees in this respect rather to the abnormal cleavage of sea urchins in $Ca^{\cdot\cdot}$-free sea water. It is, therefore, interesting to note that in the latter case also in sea urchins the blastomeres are completely surrounded by the original cortical cytoplasm, as they are by the "vitelline membrane" in *Limnaea*.

On the other hand, the observations that the vitelline membrane is partly lifted from the egg by the 2d polar body in normal development, that it wrinkles in eggs shrinking by hypotonicity, altogether may lose its connection with the egg surface in $Ca^{\cdot\cdot}$-free media, and is, probably, cast off at the 2d day in normal development, point to its agreement with similar membranes described as "vitelline membrane" or "chorion" in other eggs. We can bring this in accordancy with our previous considerations by the following quotation from Chase (1935); "The surface layer of the unfertilized egg (the vitelline membrane), while distinguishable from the underlying cytoplasm, is a part of the cortex of the egg". It is to be noted, however, that in many instances this "vitelline membrane" of unfertilized eggs is lifted afterwards from the egg surface in form of a "fertilization membrane", which is not the case in *Limnaea*.

Summarizing, we may conclude that the "vitelline membrane" of *Limnaea* forms the outer layer of the cortical cytoplasm, and corresponds at once to the "vitelline membrane" of unfertilized and the "protoplasmic surface layer" of fertilized marine eggs. Apparently, it is not that part of the egg cortex that is most active in the formation of the cleavage furrow; its function consists especially in the formation of the cell boundaries and the binding together of the blastomeres 1).

2. The cleavage cavity and its significance for the osmotic regulation of the egg

In a previous paper (Raven 1945), I have shown that the egg of *Limnaea* swells during the uncleaved stage, probably by the absorption of water, the increase in volume amounting to 35-55%.

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1) Recent experiments of Miss O. Hudig (Proc. Kon. Ned. Akad. Wetenschappen **49**, 554, 1946) have shown that the structure described above as the "vitelline membrane" consists, probably, of 2 layers of different character; the outer layer remains external to the egg and is later cast off as a true chorion; the inner folds inwards with the cleavage grooves and forms the cell boundaries.

This swelling is due to osmotic forces (RAVEN & KLOMP, 1946). Whereas the freshly laid egg is isotonic with 0.09-0.10 Mol solutions of non-electrolytes, the osmotic pressure of the egg capsule fluid, by which it is bathed, seems to be considerably less. In 0.03 Mol solutions of urea or sucrose, the eggs swell about at the same rate as in the egg capsule fluid. This might be interpreted as an indication that the osmotic pressure of the egg capsule fluid differs not much from this value; allowance must be made, however, for secondary influences of the chemical composition of the medium upon the rate of swelling.

When the eggs swell in 0.03 Mol urea or sucrose solutions, in the 4-5 hours between oviposition and 1st cleavage they do not reach their equilibrium volumes; the swelling continues at a nearly constant rate until cleavage sets in. The same holds true for the natural swelling of the eggs in the egg capsules. We may conclude, therefore, that at the moment of cleavage the internal osmotic pressure of the eggs still exceeds that of the surrounding fluid. Hence, it is likely that the swelling is continued after cleavage. As precise volume determinations become very difficult with the beginning of cleavage, in consequence of the fact that the eggs have no longer a simple geometrical shape, the process of swelling cannot be followed accurately beyond this moment.

The water absorbed by the uncleaved egg is, for a considerable part, laid down in the form of vacuoles arising at the expense of the γ-granules (RAVEN 1945). The determination of the volumes of the zones of centrifuged eggs at various moments during the uncleaved stage permitted the conclusion that these granules absorb nearly 3 times their own volume of water in the process of vacuole formation.

When the blastomeres formed at the 1st cleavage have flattened against each other with formation of a distinct cell boundary, the cleavage cavity makes its appearance. This cavity is filled with a fluid consisting, apparently, for the most part of water, though a fine coagulum visible in it in sectioned eggs indicates that it contains some proteid matter. Concerning the origin of this fluid might be thought of an intake of egg capsule fluid from the exterior. The observations that the cleavage cavity at its origin has decidedly no communication with the exterior, and that the composition of the fluid differs considerably from that of the albuminous substance surrounding the egg, speak strongly against such a supposition. Hence, the cleavage cavity fluid comes, apparently, from the blastomeres, by which it is secreted into the cavity. The observation of special secretion cones serving for this secretion of the cleavage cavity fluid strongly supports this view.

This secretion of a watery fluid into the cleavage cavity, from which it is expulsed to the exterior at regular intervals, forms the counterpart of the osmotic absorption of water by the external cell surface. Whereas the latter is, evidently, essentially a physical process obeying to the laws of osmosis, the secretion of the egg capsule fluid cannot be understood in this simple way: it is an active function of the living cell. COMANDON & DE FONBRUNE (1935) compare the blastomeres with gland cells, arranged around the cleavage cavity like those of the thyreoid around the acini filled with secretion products.

As one of the consequences of this secretion of the egg capsule fluid we can stress the fact that by it the cell discharges itself from the excess water taken up from without. As a matter of fact, after the cleavage cavity has formed the vacuolization of the protoplasm shows, in general, no further increase; on the contrary, at later cleavage stages it diminishes considerably, which leads ultimately to the almost total disappearance of the watery vacuoles, which were so abundant at previous stages. Eggs swelling in distilled water, on the other hand, in which no cleavage cavity is formed, cytolyse at the 4-cell stage under the symptoms of a vacuolar degeneration (RAVEN & KLOMP, l.c.).

The cleavage cavity in the Pulmonate egg plays, therefore, an important part in the water regulation of the egg; it may be compared, in this respect, with the kidney of Metazoa and the contractile vacuole of Protozoa (KOFOID 1895). We can guess, furthermore, that the continuous flow of water through the egg protoplasm, brought about by the endosmosis at the outer surface and the expulsion of fluid by means of the cleavage cavity, is of considerable importance for the excretion of waste-products and the respiration of the egg.

At later cleavage stages, the osmotic absorption of water from the egg capsule fluid is partially obscured by another phenomenon: the ingestion of the egg capsule fluid by the cells and its accumulation in the ectoplasmic albumen vacuoles. Probably, both processes, belonging to different spheres of cellular activity, occur simultaneously in these stages. Until the gastrula stage, the excess water taken up by endosmosis is discharged at rather regular intervals by the cleavage cavity, as has been accurately described by COMANDON & DE FONBRUNE (1935). Beyond this stage, this function is apparently taken over by the protonephridium; it is possible, however, that an intermediate stage exists, during which the head vesicle, which can be considered as a derivative of the cleavage cavity, belongs to this functional cycle of water discharge. In this phase, the eggs are very susceptible to osmotic disturbances; in suboptimal conditions, they often swell into shapeless vesicles.

3. The distribution and transformation of the proteid yolk

In the uncleaved egg, two sorts of yolk granules are present: β- and γ-granules (RAVEN 1945). The smaller β-granules are accumulated especially in the subcortical plasm, the coarse γ-granules in the inner plasm. During the uncleaved stage, the γ-granules absorb about 3 times their own volume of water, which leads to the vacuolization of the inner plasm.

At the 3d cleavage, the β-granules come to lie especially in the dense protoplasm at the animal side, the γ-granules in the vacuolated plasm of the vegetative half of the egg. Consequently, during further cleavage the β-granules are distributed with the ectoplasm, the γ-granules with the endoplasm over the cells. At the same time, the vacuolization of the endoplasm decreases, so that the γ-granules are no longer each surrounded by a vacuole.

A transformation of the proteid yolk occurs during cleavage: the β-granules are dissolved in the cytoplasm, the γ-granules increase in number. At the same time, albumen is ingested by the cells from the surrounding egg capsule fluid, and laid down in numerous albumen vacuoles in the ectoplasm. Probably, the nucleus plays a part in these transformation processes; the same holds true of the Golgi bodies. As both the β- and the γ-granules are formed during oogenesis by the activity of Golgi bodies (L. H. BRETSCHNEIDER, unpublished), the participation of the latter in their transformation is not surprising.

During further development, the γ-granules decrease in size; at the same time, their stainability changes (δ-granules). When the differentiation of the cells progresses, these granules disappear altogether.

At the same time, the ingestion of albumen from the egg capsule fluid is restricted more and more to the albumen cells of the gut. An extracellular digestion of the albumen by droplets secreted into the gut lumen by the entoderm cells is indicated from the gastrula stage; somewhat later, there is also an intracellular digestion in the vacuoles of the albumen cells, the contents of which show an acid reaction.

As development progresses, the embryos become more and more dependent upon the albumen reserve of the egg capsule fluid for their nutrition and growth. As to the composition of the latter, some preliminary determinations have been made. They show that it consists mainly of proteins giving the usual reactions; besides, a small quantity of fatty substances, staining with Scharlach R, seems to be present. No glycogen has been found.

4. The role of the nucleus in cell metabolism

When in the course of cleavage a regular distribution of ecto- and endoplasm has been attained, the ectoplasm composing the apical part and the endoplasm the basal part of the cells, the nuclei show a constant position at the boundary between both substances in all cells. In this region of the cell, considerable interactions between these portions of the protoplasm may be assumed to take place. The disappearance of the β-granules and the ingestion of albumen occurs in the ectoplasmic part of the cell; coincidently, the γ-granules in the endoplasmic part increase in number. When our supposition is right that the latter are formed by a precipitation of proteid substances originating from the first-mentioned processes, a transport of these substances from the ectoplasm to the endoplasm must take place. Moreover, when the albumen ingested from the egg capsule fluid is used in some way or other in the nutrition or growth of the cell, a chemical transformation of the ingested matter will, no doubt, occur. Hence, the position of the nucleus can be related to these processes of protein metabolism.

There are more facts pointing to a metabolic activity of the nucleus, especially with regard to protein metabolism. During oogenesis and yolk formation, the nucleus of the *Limnaea* oocyte displays signs of a considerable activity (L. H. Bretschneider, unpublished). A periodic swelling and shrinking of the nucleus is indicated; in many instances, it loses its spherical shape, forming papillary projections at one side, in which a considerable exchange of substances between nucleus and cytoplasm occurs; vacuoles, granules or colloid substances pass from the nucleus into the cytoplasm. At the same time, the nucleoli show an intense synthetic activity. Substances are produced either in the interior or at the surface of the nucleoli, and extruded into the nucleoplasm, or directly through the nuclear membrane into the cytoplasm.

Similar processes occur during the transformation and breakdown of the yolk, beginning at later cleavage stages and continuing till the trochophore stage. As a matter of fact, an epinucleolar formation of products has not been observed in these phases; but the formation of intranucleolar vacuoles is of very common occurrence. These vacuoles are extruded, apparently, into the nucleoplasm; the passage of the produced substances through the nuclear membrane into the cytoplasm has not been observed in these cells, but is likely to occur. Moreover, an extrusion of entire nucleoli into the cytoplasm is indicated clearly during cleavage and gastrulation; the extruded nucleoli fragment soon, and the fragments are dispersed among the yolk granules.

The passage of nucleolar substance into the cytoplasm has been described by many authors, especially during oogenesis. In most cases, the nucleoli fragment prior to their extrusion, and their substance passes, either in the form of fine granules or in dissolved form, through the nuclear membrane. An extrusion of entire nucleoli has been described e.g. during the oogenesis in *Cambarus* (KATER 1929), *Tegenaria* (KOCH 1929), *Eucalanus* (HEBERER 1930), various lice (RIES 1932), *Palaemon* (BHATIA & NATH 1931) and *Holothuria* (OKA 1940); furthermore, it has been recorded in many instances during secretion in gland cells (JACOBS 1929, DITTUS 1936, 1940, GRONER 1940). As far as I know, no similar processes, accompanying the breakdown of the yolk during early development, have been described in other embryos.

That the nuclei, and especially the nucleoli, play a predominant part in cell metabolism, is further indicated by their chemical composition. The nucleoli are very rich in ribonucleic acids. Recent investigations suggest that nucleoli of this kind participate in the production of cytoplasmic ribonucleic acids, which, in their turn, assist in protein synthesis (CASPERSSON 1941, HYDEN 1943). The observation that in many tissues of the *Limnaea* trochophore the cytoplasmic ribonucleic acids are most concentrated immediately around the nuclear membrane lends support to this hypothesis.

The nucleoli of later cleavage stages contain sulfhydril compounds, whereas the cytoplasmic glutathione is accumulated in the neighbourhood of the nuclei. This suggests a similar relationship between nucleolus and cytoplasm as in the case of ribonucleic acids. The papers of BRACHET (1940, 1942) on the localization of sulfhydril compounds and of ribonucleic acids during the development of the amphibia point, moreover, to a narrow topographical relationship between both reactions. It is sufficient to remind here the current notions on the significance of the sulfhydril group in oxido-reduction processes to appreciate the importance of its localization within the cell.

Similarly, the presence of iron in the nucleoli at the early trochophore stage may be brought in connection with their role in cell metabolism. Like the sulfhydril compounds, the iron atom plays a part in many oxido-reduction processes in the cell. Finally, the benzidine peroxidase, which has been observed in the nucleoli of the late gastrula stage, can be mentioned here, though its function in cell life is still rather obscure.

Together, these facts afford convincing evidence of the active role the nucleus, and especially the nucleolus, plays in cell metabolism in the developing *Limnaea* embryo.

5. The behaviour of various components of the egg during development

a. Fatty yolk

The fat droplets, which are in the uncleaved egg rather uniformly distributed through the egg protoplasm (RAVEN 1945), come to lie at the 8-cell stage especially in the vacuolated plasm; hence, they are distributed during further cleavage with the endoplasm. Consequently, the mesoderm cells are richest in fat, the entoderm gets less, the ectoderm only very few fat droplets. At the late trochophore stage, in all germ layers a further differentiation occurs: In the mesoderm, the giant excretory cell of the protonephridium is very rich in fat; in the entoderm, most fat droplets are found in the albumen cells; in the ectoderm, the cells of the velum contain many fat droplets, like those of *Aplysia* (RIES & GERSCH 1936) and of the Nudibranchs (CARTER 1928).

b. Golgi bodies

Contrary to the opinion of GATENBY (1919) and HIRSCHLER (1918), there are some indications that no direct continuity exists between the Golgi bodies of the uncleaved egg of *Limnaea* and those found in the cells of the embryo. Presumably, the Golgi bodies of the egg assist in the transformation of the proteid yolk during cleavage. Simultaneously, a new generation of Golgi bodies arises in the form of a Golgi field adjacent to the nuclei consisting of granules and rods of praesubstance. The Golgi bodies, found by GATENBY and HIRSCHLER in the gastrula, may originate from this Golgi field. In the late trochophore, the form and localization of the Golgi bodies shows specific differences in the various tissues of the embryo.

c. Mitochondria

The mitochondria (α-granules), which are located in the uncleaved egg at first in the inner protoplasm, are then accumulated in the animal pole plasm (RAVEN 1945). In this way, they come to lie in the dense protoplasm at the animal side at the 3d cleavage, and are distributed with the ectoplasm during further cleavage. Consequently, they are most numerous in the ectoderm of the gastrula, whereas the mesoderm is nearly devoid of mitochondria. With the onset of differentiation, a new arrangement occurs: Now, the large ciliary cells of the ectoderm, the albumen cells of the gut and the protonephridium become rich in mitochondrial substances, whereas the other tissues contain only few mitochondria.

d. Glycogen

At the 24-cell stage, there is a remarkable accumulation of glycogen in the central plasm, where all blastomeres meet with their central ends. At later cleavages stages, the cells 4a-4c and their descendants are especially rich in glycogen; the rest of the entoderm and the mesoderm contain only little glycogen. Though at the early gastrula stage a rather sharp limit, separating two regions with different glycogen contents of the cells, is found near the blastoporal margin, this has nothing to do with the similar limit present in Amphibia (WOERDEMAN 1933, RAVEN 1933, 1935) and birds (JACOBSON 1939), where it is brought about by the sudden disappearance of the glycogen in the invaginated cells. There are no indications of a similar glycogenolysis accompanying invagination in *Limnaea*. With differentiation, a special accumulation of glycogen occurs in the ciliated cells of the ectoderm and in the protonephridium, whereas the other tissues are only poor in glycogen.

e. Thymonucleic acid

In the course of development, a considerable increase in thymonucleic acid contents of the *Limnaea* egg occurs. This is not only due to the augmentation of nuclear substance during cleavage (rise of the nucleoplasmic ratio), but moreover there is a marked increase of the thymonucleic acid contents of the individual nuclei. Whereas during the first stages of development only the chromosomes during mitosis are Feulgen-positive, whereas the resting nuclei and prophases do not stain in Feulgen preparations, at later stages also the latter contain thymonucleic acid. The same phenomenon has been observed in sea urchin, *Barnea*, *Rana* and axolotl (Brachet 1933).

With differentiation, a difference in thymonucleic acid contents appears between the various tissues of the embryo. The nuclei of the ectodermal ciliated cells and of the giant excretory cell of the protonephridium are very poor in thymonucleic acid, contrary to those of the other tissues.

f. Ribonucleic acid

In the uncleaved egg, ribonucleic acids are present diffusely in the cytoplasm and bound, in a higher concentration, in the β-granules (Raven 1945). With the latter, they are distributed in greater quantity to the subcortical plasm of the egg, then to the ectoplasm of the cleavage cells.The nucleoli seem to be centres of ribonucleic acid formation; furthermore, a considerable accumulation of these acids is found in special dark bodies in the central part of the cells of the 4th quartette, arising from the concrescence of particular cytoplasmic granules. In the trochophore, a differential distribution of ribonucleic acids occurs. The ciliated cells of the ectoderm are nearly devoid of these substances, the albumen cells of the gut and the protonephridium have a cytoplasm poor in ribonucleic acid; the other tissues have a high concentration of these substances. Moreover, specific differences in their intracellular localization between the cells of different tissues exist.

Hence, the ripe egg of *Limnaea* agrees with that of sea urchins (Brachet 1940) in containing a great quantity of ribonucleic acids in its cytoplasm, contrary to those of Amphibia, *Drosophila* and *Planaria*, where a decrease of these acids occurs during oogenesis (Brachet 1942). Probably, these substances form a nucleotide reserve permitting the rapid synthesis of thymonucleic acid during development (BRACHET 1933, 1935; PAINTER 1940). Moreover, they may play a part in growth, especially cell division, and protein synthesis (CASPERSSON & SCHULTZ 1939, CASPERSSON 1940, 1941; BRACHET 1942). In this respect, it is interesting to note that in the *Limnaea* trochophore the tissues in which cell division has come to an end (ciliated cells, albumen cells, protonephridium) are poor in ribonucleic acid, whereas the other, rapidly dividing tissues still contain a considerable quantity of these substances. Similarly, in *Rana* KEDROWSKI (1937) notes the absence in several highly differentiated and non-dividing cells (pigment cells, blood cells) of his "acid anabolites", which also may be ribonucleic acids (DUSTIN 1944).

Presumably, the total ribonucleic acid contents of the *Limnaea* trochophore exceed many times that of the ripe egg. Hence, a synthesis of these substances during development must be assumed. In this synthesis, the nucleoli of the cells may play a part (CASPERSSON 1941, HYDEN 1943). This is indicated by their high ribonucleic acid contents in most tissues of the embryo, and by the fact that often the cytoplasmic ribonucleic acids have their highest concentration immediately adjacent to the nuclear membrane.

g. Sulfhydril compounds

The free glutathione, present in the uncleaved egg of *Limnaea* in the neighbourhood of the maturation spindle (RAVEN 1945), is derived from the germinal vesicle, which is rich in this substance at the end of oogenesis (L. H. BRETSCHNEIDER, unpublished). In this respect, the *Limnaea* egg agrees with those of many other animals (BRACHET 1940). At cleavage stages, the cytoplasmic glutathione remains most concentrated in the neighbourhood of the nuclei. Finally, the ectoderm is rich in glutathione, the entoderm nearly devoid of it.

Sulfhydril compounds bound to proteids are present in the whole uncleaved egg, especially in its central part (RAVEN 1945); moreover, a strong accumulation of SH-compounds is found in the egg cortex. At cleavage stages, the ectoplasm is richer in these substances than the endoplasm; in the nuclei, the nucleoli are characterized by their abundance in sulfhydril compounds. At the late gastrula stage, they are especially accumulated in the entoderm; in the trochophore, also the mesoderm cells are rather rich in these substances, the ectoderm much less.

From these observations, there is no reason to suppose that the sulfhydril compounds play a prominent part in determination, as is supposed by BRACHET (1940) to be the case in Amphibia.

h. Indophenol oxidase

In the eggs of *Nereis* (REVERBERI & PITOTTI 1940), *Tubifex* (LEHMANN 1941), *Aplysia* (RIES 1937) and the Ascidia (RIES 1937, 1939; REVERBERI & PITOTTI 1939) the indophenol blue oxidase shows a local accumulation, in consequence of which it is distributed during cleavage to special parts of the embryo. In *Limnaea*, however, no local accumulation of indophenol blue oxidase occurs till a rather late stage of development. There is no reason, therefore, to think that this substance has anything to do with the early determination of the cells in this form. At the late gastrula stage, an elective reaction of the velum and head vesicle occurs. At still later stages, the reaction is especially localized in the shell anlage and the mantle fold; moreover, subepidermal cells crowded with indophenol blue granules appear. An elective indophenol blue reaction of the ciliary apparatus has been observed in *Aplysia* (RIES 1937) and *Hydroides* (REVERBERI & PITOTTI 1940), of the shell anlage in *Aplysia* (RIES 1937). VAN HERWERDEN (1923) found indophenol blue oxidase in the mantle of *Limnaea ovata*, and thought that it played a role in the formation of the pigment bands of the shell.

i. Benzidine peroxidase

A local accumulation of benzidine peroxidase has been recorded by RIES (1937, 1939) in the eggs of *Aplysia* and the Ascidia, by REVERBERI & PITOTTI (1940) in *Nereis* and by PITOTTI (1939) in sea urchins (cf. however LINDAHL 1941). In *Limnaea*, no such regional accumulation has been observed until the late gastrula stage. At this stage, a strong elective reaction of 2 pairs of cells at the lateral angles of the embryo, representing, probably, the descendants of the anterior trochoblasts, occurs; the velum and head vesicle react more weakly. In all cells, the nucleoli are heavily stained. At the late trochophore stage, the gut also shows a rather strong benzidine peroxidase reaction; still later the reaction is localized in the mantle fold, the shell, and particular mesenchyme cells in the interior of the embryo. Hence, the localization of the benzidine peroxidase reaction varies according to the stage of development; with progressing differentiation, in different groups of cells the enzyme shows a maximum of activity. It seems, therefore, that this peroxidase plays a part in cellular differentiation; there are no indications, on the other hand, that it has anything to do with the primary determination of the germ layers and organs of the embryo.

An elective benzidine peroxidase reaction in the ciliary apparatus has been observed in the larvae of molluscs, Annelids and Bryozoa and in adult Rotifers (PRENANT 1924); in larvae of sea urchins (PITOTTI 1939), *Hydroides* and *Eucharis* (REVERBERI & PITOTTI 1940). PRENANT denies its presence in the velum of *Limnaea*, but has, evidently, overlooked its localization in early stages of the latter. In the gut, it has been recorded in *Aplysia* (RIES 1937), *Hydroides* (REVERBERI & PITOTTI 1940) and sea urchins (PITOTTI 1939). An elective reaction of the mantle fold in *Limnaea* has been recorded already by PRENANT (1924); in *Planorbis*, it is located more diffusely in the shell. The presence of peroxidases in the shell may be connected with the formation of shell pigments (Cf. PRENANT 1924; VOINOV & VOINOV 1924).

k. Iron

The uncleaved egg of *Limnaea* contains a large quantity of free iron; it is accumulated especially in the β-granules (Miss E. EXALTO, unpublished). At later stages, a progressive decrease of iron occurs; at first, the small ectoderm cells lose their iron contents, then the mesenchyme and the entoderm. A considerable amount of iron granules remains till late stages in the protonephridium and the ectodermal ciliary cells; in the last days before hatching, however, also in the latter the non-masked iron disappears. As no determinations of masked iron have been made, it is not certain whether the iron has been lost from the embryo or has been laid down in another form.

l. Vital staining experiments

The uncleaved eggs of *Limnaea*, when stained with basic vital dyes, show a rather weak diffuse staining (RAVEN 1945). It is not certain, to which elements of the egg the dye is bound; from the fact that the clear polar area remains colourless we may deduce that it is no diffuse staining of the hyaloplasm, but that we have to do with a granular staining of the yolk. In neutral red after prolonged staining a ring of red granules appears at the margin of the clear polar area; these "Speichergranula" may derive from the mitochondria (RIES & GERSCH 1936; GERSCH &

RIES 1937). At the 8-cell stage, an elective staining of the dense animal plasm has been observed in brilliant cresyl violet only. At later stages, the basic dyes are accumulated in the albumen vacuoles of the cells. These vacuoles may be considered to represent PARAT's "vacuome" (PARAT 1928). They have a definite localization within the cells, being restricted to their ectoplasmic parts; they can be stained with basic dyes; their contents are proteidic in nature, and they contain no fatty or lipoidic substances; all characteristics of the "vacuome" after PARAT. As a matter of fact, they are not impregnated by osmium or silver, but these are properties of the Golgi bodies which are identified by PARAT with the vacuome, an identification which is, however, repudiated recently by most authors (cf. HIRSCH 1939). Furthermore, KEDROWSKI (1932) has shown that in many instances proteolytic and proteid-forming processes can be proved to go on in the "vacuome"; it is likely that in these cases cell proteases are secreted into the vacuoles and activated in this way. This is in good agreement with my observations in *Limnaea*, which prove that, at least at later stages of development, a digestion of the albumen in the vacuoles of the entoderm takes place.

There exist some differences between the basic dyes as regards their staining properties. Neutral red is accumulated exclusively in the albumen vacuoles; the yolk granules remain colourless. Nile blue hydrochloride stains, besides the albumen vacuoles the yolk granules in green and the mitochondria in deep blue. In brilliant cresyl violet the contents of the albumen vacuoles do not stain uniformly, as in the former dyes, but the dye is precipitated in a granular form in the vacuoles; moreover, the cytoplasm is diffusely stained, but the yolk granules and mitochondria remain colourless.

As methylene blue and Janusgreen do not penetrate into intact cells, no vital staining of the *Limnaea* embryo can be performed with them. Postvitally methylene blue gives a diffuse staining of the cytoplasm and the nucleoles; at later stages, it stains the shell rudiment. Janusgreen stains postvitally the mitochondria, the γ-granules and the nucleoli.

6. Presumed gradient-field actions in the development of Limnaea

Recent advances in experimental embryology have afforded convincing evidence of the preeminent role gradient-fields play in early development (Dalcq 1941). Such fields, which may have different configurations (cf. Raven 1943), are supposed to be responsible for the primary chemodifferentiation of the eggs in various groups. Experiments on the influence of lithium upon the development of *Limnaea* (Raven 1942) have led to the conclusion that also in this form gradient-field actions must be admitted.

As a matter of fact, such actions can only be deduced from an experimental analysis of development; a descriptive study of the phenomena of normal development, like the present, can afford no proof of their existence. On the other hand, such a study can prepare the way for the experimental analysis by showing which processes of normal development would be comprehensible in the light of the presumed existence of gradient-fields. Therefore, in this chapter I will resume all phenomena of normal development which could be explained by the admission of the existence of special gradient-fields. It is, in other words, by no means pretended that the processes enumerated below prove the existence of gradient-fields; it will be necessary to investigate with regard to every one of them if such an explanation holds true.

In general, these phenomena constitute directed movements of cell components. In a gradient-field, a system of directed forces (gradients) exists, in such a way that to every point of the field at least one of the gradients can be assigned; every point is, therefore, characterized by at least one prevalent direction. Therefore, it can be hoped that a better knowledge of the laws governing gradient-field actions will throw some light on the causes of directed movements which are of such importance in early development.

We shall restrict ourselves with regard to the phenomena of development to the period between oviposition and gastrulation. At later stages, especially with the beginning of differentiation, the developmental processes attain a degree of complexity which makes even their preliminary classification a matter of considerable difficulty.

The directed movements of cell components can be related to a system of coordinates pervading the entire egg. The first of these is 1. the major egg axis, traversing the egg from the animal to the vegetative pole. 2. The dorsoventral axis is perpendicular to it, whereas 3. the transverse axis can be drawn at right angles to both of them. There are, however, movements of cell components which cannot be related to any of the 3 axes mentioned before, but which can only be understood by bringing them in connection with a fourth category of directions, which may be called 4. extero-interior. Thus, the phenomena under consideration fall into 4 classes: animal-vegetative, dorso-ventral, left-right and extero-interior polarity.

A. Animal-vegetative polarity

The following processes can be brought under this title:

1. The accumulation of the subcortical protoplasm at the vegetative pole, occurring, apparently, during the last hours before oviposition. It is of relatively short duration; immediately after oviposition, the subcortical plasm begins to shift its position, its ultimate distribution being determined, apparently, by the extero-interior polarity of the egg (cf. below). Whether the factors bringing this plasm to the vegetative pole are no longer in action after oviposition, or new and more powerful influences exert their action upon it from this moment on, remains to be investigated.

2. The ascent of the maturation spindle to the animal pole occurs also in the last hours before oviposition, during the passage of the egg through the oviduct (L. H. Bretschneider, unpublished). Arrived in the neighbourhood of the animal pole,

3. the spindle places itself along the egg axis. It may be presumed that both phenomena together determine the site of the next steps:

4. the extrusion of the 1st polar body at the animal pole,

5. the reconstitution of the maturation spindle at this place,

6. the extrusion of the 2d polar body at the animal pole, and

7. the formation of the female pronucleus at the same place.

After moderate centrifuging, the polar bodies are extruded at the original animal pole of the egg, irrespective of the direction of stratification. This indicates that this series of developmental processes (2-7) is directed by attractive forces residing in the relatively immovable egg cortex.

8. The ascent of the spermaster to the animal pole is followed by

9. the movement of the male pronucleus to this pole, where it meets the female pronucleus. In view of what is known to be the case in other eggs, the latter process may rather be due to attractive forces exerted by the female pronucleus than to directive influences of the egg polarity.

With regard to

10. the formation of the animal pole plasm, we know with certainty that there are localizing actions which bring about this phenomenon (RAVEN 1945); it is most likely that they consist of attractive forces residing in the egg cortex at the animal side, which are responsible for the accumulation of this plasm not only in normal eggs, but likewise in eggs submitted to centrifugation immediately after oviposition. On the other hand, it is probable that the centripetal flow of protoplasm to the centre of the maturation aster, dilating prior to its final reduction, assists in this process; in this way, it is linked to the preceding phenomena.

Special mention has to be made of

11. the accumulation of α-granules in the animal pole plasm; in eggs centrifuged immediately before cleavage, these granules, which have been heaped up in a middle zone of the stratified egg, return in a large proportion to the animal side of the blastomeres (RAVEN, in the press).

12. The formation of the 1st cleavage spindle immediately beneath the animal pole may be a consequence of the position of the pronuclei. In its turn, it is one of the factors bringing about that

13. the cleavage furrow begins at the animal pole. Whereas the spindle remnant is displaced by the advancing cleavage furrow in a vegetative direction,

14. the cleavage nuclei remain behind in the neighbourhood of the animal pole.

At the 2d cleavage, the same phenomena may be mentioned:

15. the cleavage spindles are formed near the animal side of the blastomeres,

16. the cleavage furrows begin at the animal pole, and

17. the cleavage nuclei formed at this cleavage retain an animal position.

Prior to the 3d cleavage,

18. the subcortical plasm flows in an animal direction and is heaped up at the animal pole, uniting with the

animal pole plasm and the perinuclear plasm. Presumably, the subcortical plasm comes once more under the influence of the animal-vegetative gradient of the egg.

19. The 3d cleavage spindles are formed in the animal half of the blastomeres, their longitudinal axis being perpendicular to those of the preceding cleavage. Their position determines

20. the unequal division of the blastomeres into a macromere and a micromere.

At the next divisions, the picture of cleavage becomes too complicated to be followed step after step with the same accuracy. Some points may still be noted:

21. In general, in each division the distribution of substances is such that the animal daughter cell gets more of the dense ectoplasm, the vegetative cell more of the vacuolar endoplasm. This brings about the differential distribution of ecto- and endoplasm, which is characteristic of later cleavage stages.

22. The ingestion of albumen begins in the animal half of the egg, somewhat later at the vegetative side.

23. At the end of the period of cleavage, a depression appears at the animal pole of the egg.

24. In the centre of this depression in a few cells giant albumen vacuoles appear.

25. Finally, the invagination of the archenteron begins at the vegetative pole.

The processes listed above are certainly no mutually independent phenomena; they are linked in multiple ways, as indicated above. E.g. the numbers 2-9, 12-17 and 19-20 form one uninterrupted series of events, in which every former member conditions the next.

Summarizing, it may be said that the phenomena of normal development suggest that the animal-vegetative gradient-field of the egg acts

1°. on the nuclear and mitotic apparatus, determining its position in the neighbourhood of the animal pole during the first 3 cleavage cycles, and cooperating in the determination of the direction of the cleavage spindles in these and later cleavages;

2°. on the subcortical plasm, causing its accumulation at the vegetative pole prior to oviposition, and its attraction to the animal side immediately before the 3d cleavage. In the mean time, the subcortical plasm obeys to other influences.

3°. on the animal pole plasm (and the α-granules), attracting it to the animal side in the last hour before the 1st cleavage;

4°. on the ecto- and endoplasm, determining their differential distribution during the later phases of cleavage.

B. Dorso-ventral polarity

Whereas the *Limnaea* egg shows from the beginning a clearly marked animal-vegetative polarity, the visible signs of its dorso-ventral differentiation appear later and are by far less obvious. The first phenomenon, which can be considered in this respect is

1. the direction of the first cleavage spindle, which in its turn determines the direction of cleavage, separating the left anterior and right posterior blastomeres AB and CD, respectively.

The same holds true for

2. the direction of the 2d cleavage spindles.

Perhaps the observation that often

3. the 2d cleavage furrows begin somewhat earlier in one of the blastomeres should be mentioned here, too; it has not been determined whether AB or CD is the first to begin with cleavage, or the difference is only casual.

4. The formation of the animal and vegetative cross furrows at the 4-cell stage is also related to the dorso-ventral polarity.

Similar considerations can be applied to further cleavage. In general, it may be said that

5. the pattern of cleavage testifies the existence of dorso-ventral polarity. Particularly, I will mention

6. the formation of the M-blastomere from the posterior macromere, and

7. the differential distribution of the glycogen in the cells of the 4th quartette, excepting the M-blastomere.

More obvious phenomena of dorso-ventral differentiation occur beginning with the gastrula stage; they will, however, not be considered here.

Summarizing, it may be concluded that the action of the hypothetical dorso-ventral gradient-field in the early stages of development expresses itself preeminently in the determination of the position and direction of the cleavage spindles, which in their turn govern the pattern of cleavage. Furthermore, the distribution of glycogen seems to be, directly or indirectly, related to this field.

C. Left-right polarity

Similarly, the left-right polarity of the egg finds its expression during early development in the asymmetrical pattern of cleavage, which can, therefore, be thought to be determined by the interaction of the animal-vegetative, dorso-ventral and transverse gradients of the egg. At later stages, this polarity determines the asymmetrical development of the body of the snail.

D. Extero-interior polarity

The following phenomena can be related to the extero-interior polarity of the egg:

1. At insemination, the fertilizing sperm penetrates entirely into the egg, traverses the cytoplasm and comes to rest with the sperm head immediately under the egg cortex (L. H. BRETSCHNEIDER, unpublished). This subcortical position of the sperm head is retained until the maturation divisions have been finished; then it moves to the spermaster to be transformed into the male pronucleus.

2. The subcortical protoplasm, at oviposition accumulated at the vegetative pole, begins to extend subcortically in animal direction until it surrounds the inner plasm entirely, and forms a layer of nearly equal thickness around the egg. Apparently, during this period it is especially under the influence of the extero-interior polarity.

3. In the prophase nuclei of early cleavage stages, the chromatin is heaped up in the outer part of the nucleus.

4. The formation of the central plasm at the inner end of the blastomeres at the 24-cell stage and

5. the accumulation of glycogen in this plasm.

6. The distribution of ecto- and endoplasm within the cleavage cells, is a clear expression of this polarity. More generally, the same can be said of

7. the intracellular stratification of structures and

substances: albumen, vacuoles, nucleus, Golgi-field, mitochondria, fat droplets and γ-granules. With regard to the fat droplets, it has been observed that in eggs centrifuged a short time before the 1st cleavage, in which the fat is accumulated superficially, the fat droplets retire to the inner parts of the cells during the later phases of cleavage (RAVEN & BRETSCHNEIDER 1942).

8. The direction of the cleavage spindles in the divisions, by which the primary (and secondary) mesomeres are formed, can be related to the same polarity.

9. Furthermore, the position of the "ectosomes" at the inner ends of the macromeres and of the cells of the 4th quartette, and

10. that of the fine granules, found in the same locality at the 120-cell stage, may be mentioned here.

Summarizing, it can be said that nearly all cellular structures, both nuclear and cytoplasmic, in their turn are influenced by the extero-interior polarity, which at later stages corresponds to the apico-basal polarity of the cells.

7. Chemodifferentiation and chemical differentiation

Considering the results of our analysis of the "chemical embryology" of *Limnaea*, we can clearly distinguish between two classes of events, differing considerably in their importance with regard to the determination of early development.

The first of these is the "chemo-differentiation" in the sense of HUXLEY; it may be defined as the production of (physico-) chemical differences between various parts of the embryo in early development, determining in their turn differences in developmental potencies and bringing about, in this way, the early determination of the parts of the embryo. The use of this term is confined by its author to the early stages of development, preceding the visible histological differentiation of the cells (cf. HUXLEY & DE BEER 1934, p. 195 and 440).

On the other hand, we can consider the appearance of chemical differences coincidently with the histological differentiation. In this case, the physicochemical changes cannot be regarded, without further evidence, as the causes of the morphological differentiation; it is more likely that both kinds of processes, physico-chemical and morphological, are produced simultaneously by common factors in preceding stages of development. This class of events will be called the "chemical differentiation" of the embryo.

The following processes, observed in *Limnaea* during early development, may be considered to belong to the chemodifferentiation of the embryo:

1. The displacement of the subcortical plasm from the vegetative pole of the freshly laid egg to form a subcortical layer of uniform thickness during the uncleaved stage.
2. The formation of the animal pole plasm by a cortical attraction of substances, which had been more uniformly distributed through the egg at earlier stages.
3. The animal concentration of the subcortical plasm and its fusion with the animal pole plasm and the perinuclear plasm prior to the 3d cleavage.
4. The differential distribution of the ecto- and endoplasm, formed in this way, during the subsequent cleavage divisions.
5. The accumulation of particular granules, rich in ribonucleic acid, at the central end of the macromeres, where they fuse into the "ectosomes", and their transmission into the cells of the 4th quartette at the next division.
6. The formation of the "central plasm" at the inner end of the blastomeres at the 24-cell stage.
7. The accumulation of glycogen in this "central plasm" and its transmission to the cells 4a-4c.

There are, no doubt, many more processes involved in the chemodifferentiation of the embryo, which have escaped observation in this study, because of the only restricted number of cytochemical methods employed. Still, from the results of our investigation, defective as it may be, we get an impression of the importance of the distribution of substances, brought about in this way, for the segregation of the germ layers. The mesomeres, which possess no ectoplasm, in consequence of the direction of the divisions by which they have been formed, lose their connection with the surface and form the mesoderm; furthermore, the primary mesomere differs from all other cells of the embryo by the possession of an "ectosome", but only a small quantity of glycogen. The cells at the vegetative pole, containing only little ectoplasm, change their form, which leads to the invagination of the archenteron and to their displacement into the interior, where they become entoderm. The cells of the animal half of the embryo, which are richest in ectoplasm, remain at the surface and give the ectoderm. These facts suggest that there exists a relation between the composition of the cells and their further development. Especially the proportion between ecto- and endoplasm seems to be important for the fate of the cells.

The chemical differentiation is much more obvious. The histological differentiation is accompanied with the appearance of considerable differences in chemical composition between the cells of different tissues. It is a remarkable fact that this leads in each of the 3 germ layers to the formation of 2 types of cells, which are specialized in different directions; the corresponding cell types of different germ layers have many points in common, whereas they differ in the same respects from the other cells of their own germ layer. Table I summarizes these observations:

TABLE I

		Cell type I	*Cell type II*
Comprises	in ectoderm	large ciliary cells	skin epithelium
	in entoderm	albumen cells	gut epithelium
	in mesoderm	protonephridium	mesenchyma
Furnishes		larval organs	imaginal organs
Cell size		large	small
Cell divisions		stopped	continued
Albumen vacuoles		preserved or enlarged (exc. protonephridium, where never alb. vac. present)	reduced
Golgi substance		much	little
Mitochondria		many	little or no
Fat		more	less
Glycogen		much (exc. albumen cells)	no
Non-masked iron		much	little or no
Thymonucleic acid		little (exc. albumen cells)	much
Ribonucleic acid		little or no	much

It is reasonable to suppose that the chemical differences between both cell types are connected with cell metabolism, which in its turn is related to the function and fate of the cells. The larval organs (ciliary cells, albumen digestion cells and protonephridia) need for their functional activity the presence of combustible substances (fat, glycogen), which are piled up in great quantity in their cytoplasm. The intensity of metabolic processes is mirrored by the great development of the structures of cell metabolism (vacuome, Golgi bodies, mitochondria, iron). On the other hand, these cells have lost the powers of growth and cell division; their metabolism is adjusted to the production of external goods (substances, energy), not to that of living matter. The cells of type II, on the contrary, which have to build up the entire body of the adult snail, are especially disposed towards the synthesis of living protoplasm. Their richness in ribonucleic acid stands in connection with protein synthesis; the abundance of thymonucleic acid in the nuclei may be regarded as an expression of their important presumptive fate.

Hence, the two cell types resulting from chemical differentiation in *Limnaea* can be regarded as representatives of 2 different directions of cell life. In this respect, they may have a more general importance. It has to be awaited whether comparable differences of cell type will be found in other organisms.

SUMMARY

1. The development of *Limnaea stagnalis* from the first cleavage till the trochophore stage has been studied with various cytochemical methods.

2. The uncleaved egg is surrounded by a vitelline membrane. At cleavage this membrane is carried inward with the cleavage furrows; it forms a partition wall separating the blastomeres. The cleavage cavity arises by a splitting of this wall. Apparently, the vitelline membrane of *Limnaea* is a layer of living protoplasm forming the outer layer of the egg cortex.

3. The cleavage cavity, which is formed by the coalescence of several lenticular spaces between the blastomeres, widens by the secretion of fluid into this cavity by special secretion cones on the adjacent sides of the blastomeres. The fluid is expulsed to the exterior at regular intervals. In this way, the cleavage cavity plays an important part in the water regulation of the egg.

4. Prior to the 3d cleavage, the subcortical plasm of the egg, which formed a subcortical layer of uniform thickness at earlier stages, concentrates at the animal side and fuses with the animal pole plasm and the perinuclear protoplasm to a common mass of dense protoplasm; the rest of the egg consists of vacuolar protoplasm. Both substances are distributed unequally over the cells at further cleavage; the dense protoplasm, forming the ectoplasm of all cells, is most abundant in the animal blastomeres and decreases in a vegetative direction, whereas the vacuolar proto-

plasm, which forms the endoplasm, is most abundant at the vegetative side. The ectoplasm is rich in α-granules (mitochondria) and β-granules; the endoplasm in γ-granules and fat droplets.

5. During cleavage and gastrulation, the nuclei have a constant position at the boundary between ectoplasm and endoplasm. The nucleoli show an intense activity; intranucleolar vacuoles are formed, which are extruded, apparently, into the nucleoplasm. An extrusion of entire nucleoli into the cytoplasm is indicated. The nucleoli are rich in ribonucleic acids, sulfhydril compounds, iron and benzidine peroxidase. The cytoplasmic ribonucleic acids and glutathione are, in many cells, most concentrated in the neighbourhood of the nuclear membrane. These facts point to an active role of the nucleus, and especially the nucleolus, in cell metabolism.

6. During later cleavage stages, a transformation of the proteid yolk occurs; the β-granules are dissolved in the cytoplasm, the γ-granules increase in number. At the same time, albumen is ingested by the cells from the surrounding egg capsule fluid, and laid down in numerous albumen vacuoles in the ectoplasm. Probably, the nucleus plays a part in these transformation processes; the same holds true of the Golgi bodies. During further development, the γ-granules decrease in size; ultimately, they disappear altogether. The ingestion of albumen is restricted more and more to the albumen cells of the gut. Both extracellular and intracellular digestion of albumen can be observed.

7. Probably, no direct continuity exists between the Golgi bodies of the uncleaved egg and those found in the cells of the embryo.

8. In the course of development, there is a marked increase of the thymonucleic acid contents of the nuclei.

9. Particular granules, rich in ribonucleic acid, accumulate at the central end of the macromeres, where they fuse into single dark bodies; these bodies are transmitted into the cells of the 4th quartette at the next division; at later stages, they disappear.

10. Glycogen is accumulated in the "central plasm" at the 24-cell stage; at later stages, especially the cells 4a-4c and their descendants are rich in glycogen.

11. Four equatorial groups of thickened ringlets are formed on cells of the 2d quartette during cleavage.

12. With basic vital dyes, in early stages a weak granular

staining of the yolk occurs. At later stages, the basic dyes are accumulated in the albumen vacuoles of the cells which may be considered to represent a "vacuome" in the sense of PARAT. Nile blue hydrochloride stains, furthermore, the yolk granules and mitochondria; brilliant cresyl violet gives a diffuse staining of the cytoplasm. Methylene blue and Janusgreen do not penetrate into intact cells.

13. Probably, there exists a relation between the composition of the cells and their further development; especially, the proportion between ecto- and endoplasm seems to be important for the fate of the cells.

14. At the late gastrula stage, the velum and head vesicle show an elective indophenol oxidase reaction; at still later stages, the reaction is especially localized in the shell anlage and mantle fold and in special subepidermal cells of the mesenchyme.

15. At the late gastrula stage, a strong elective benzidine peroxidase reaction of 2 pairs of cells at the lateral angles of the embryo, representing, probably, the descendants of the anterior trochoblasts, occurs; the velum and head vesicle react more weakly. At the late trochophore stage, the gut shows also a rather strong reaction; still later, it is localized in the mantle fold, the shell, and particular mesenchyme cells in the interior of the embryo.

16. The histological differentiation is accompanied with the appearence of considerable differences in chemical composition between the cells. This leads in each of the 3 germ layers to the formation of 2 types of cells: 1. large cells, without cell division, with albumen vacuoles, many Golgi bodies, mitochondria and fat droplets, rich in glycogen and iron, but poor in thymo- and ribonucleic acid; they form the larval organs (ciliary cells, albumen cells, protonephrideum); 2. small, dividing cells, without albumen vacuoles, poor in Golgi substance, mitochondria, fat, glycogen and iron, but rich in thymo- and ribonucleic acids; they have to build up the body of the adult snail. These two cell types can be regarded as representatives of 2 different directions of cell life.

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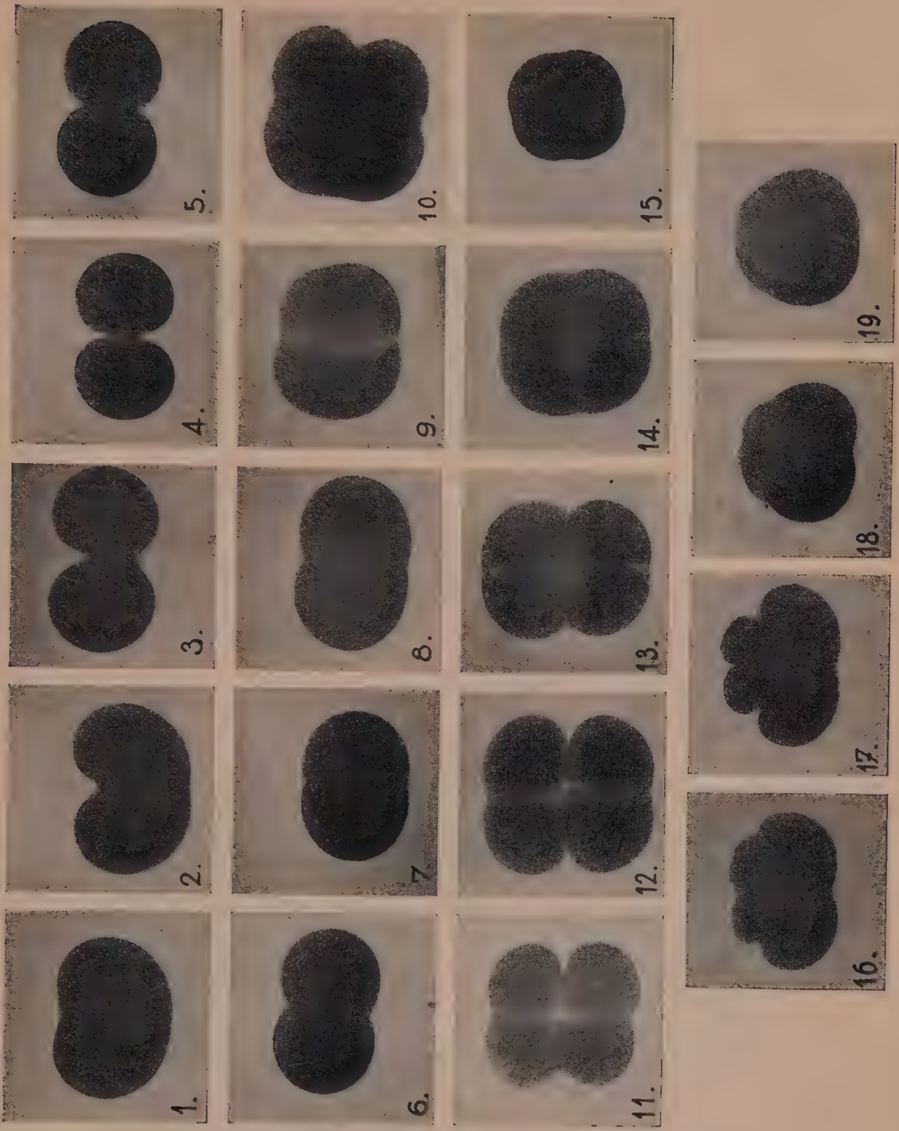

Fig. 1. Early cleavage of *Limnaea stagnalis*. 1. Beginning of the 1st cleavage groove. 2. 4 minutes later, 3. 6 minutes, 4. 13 min., 5. 31 min., 6. 38 min., 7. 56 min., 8. 66 min., 9. 114 min., 10. 119 min., 11. 133 min., 12. 142 min., 13. 148 min., 14. 159 min., 15. 181 min., 16. 210 min., 17. 216 min., 18. 225 min., 19. 235 min. after beginning of cleavage.

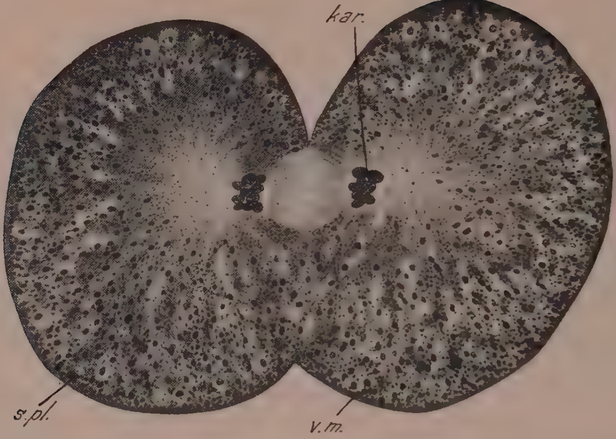

Fig. 2. Egg of *Limnaea stagnalis*. First cleavage. Stage 3. *kar.* = karyomeres of cleavage nuclei. *s.pl.* = subcortical protoplasm. *v.m.* = vitelline membrane.

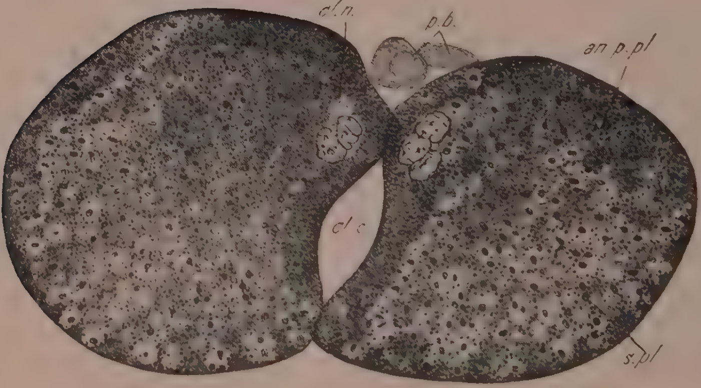

Fig. 3. Egg of *Limnaea stagnalis*. Stage 6. Formation of cleavage cavity (*cl.c.*) Karyomeres fused into larger vesicles (*cl.n.*). *an.p.pl.* = animal pole plasm. *s.pl.* = subcortical plasm. *p.b.* = polar bodies.

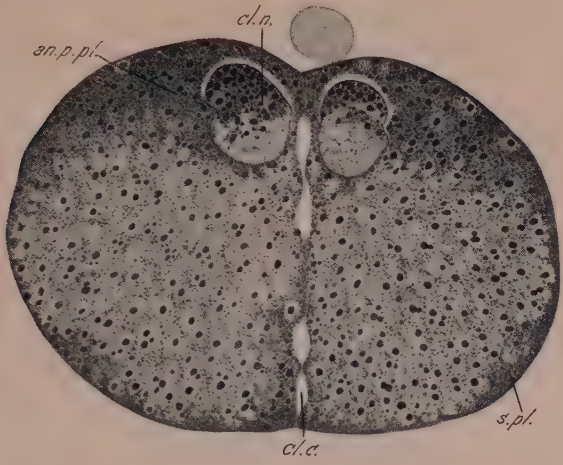

Fig. 4. Egg of *Limnaea stagnalis*. Stage 7. Beginning formation of cleavage cavity (*cl.c.*). Cleavage nuclei (*cl.n.*) in prophase, with eccentric disposition of chromatin. Further explanation cf. fig. 3.

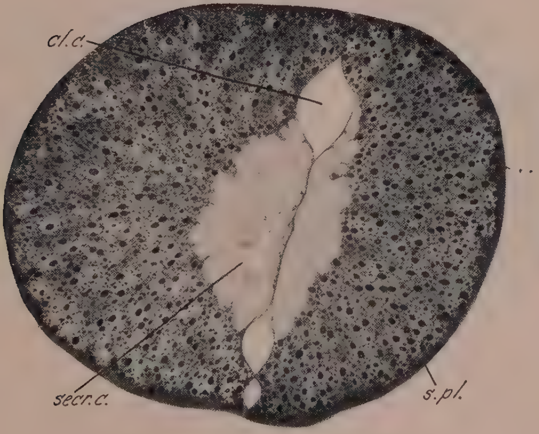

Fig. 5. Egg of *Limnaea stagnalis*. Stage 7. Formation of secretion cones (*secr.c.*) protruding into cleavage cavity (*cl.c.*).

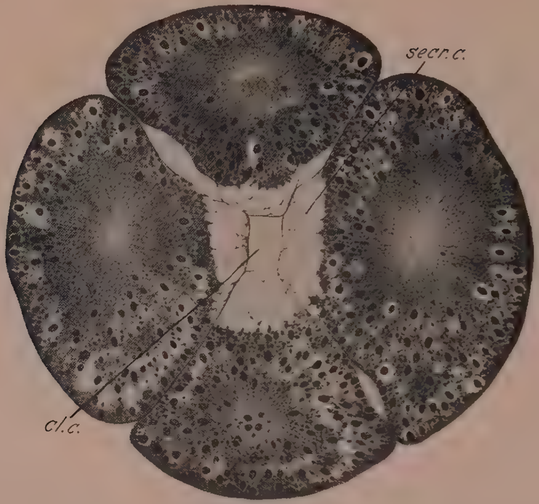

Fig. 6. Egg of *Limnaea stagnalis*. Stage 13. Secretion cones (*secr.c.*) protruding into cleavage cavity (*cl.c.*).

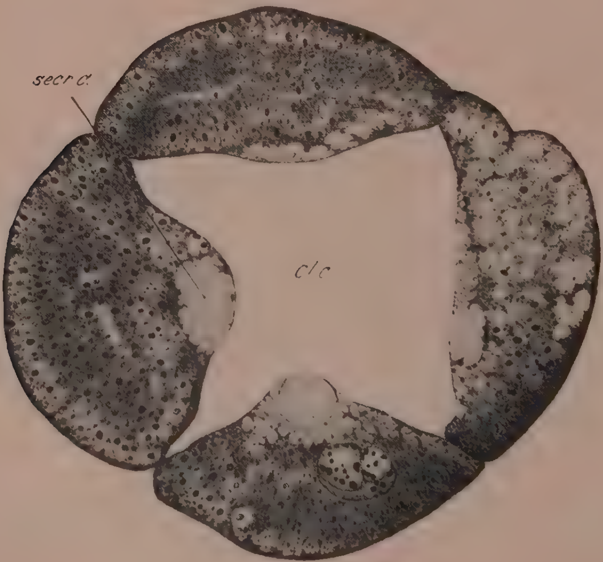

Fig. 7. Egg of *Limnaea stagnalis*. Stage 14. Cleavage cavity (*cl.c.*) much distended; secretion cones (*secr.c.*) considerably reduced.

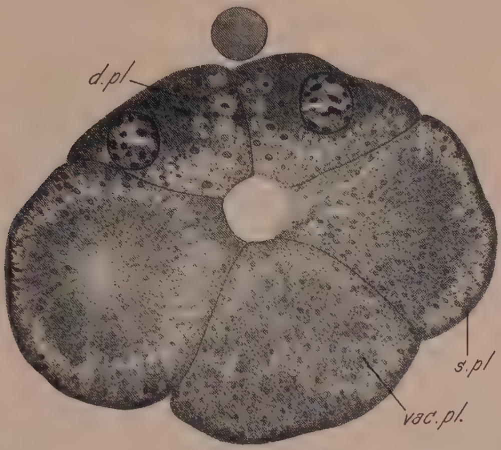

Fig. 8. Egg of *Limnaea stagnalis*. Stage 18. Micromeres consisting mostly of dense protoplasm (*d.pl.*), macromeres of vacuolar plasm (*vac.pl.*).

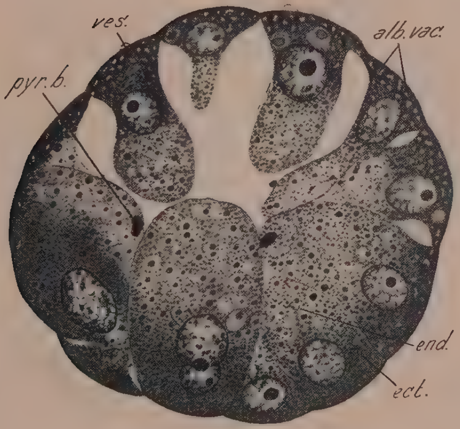

Fig. 9. Egg of *Limnaea stagnalis*, ± 40-cell stage. Blastomeres consisting of ectoplasm (*ect*) and endoplasm (*end*). Albumen vacuoles (*alb.vac*) in ectoplasm of animal blastomeres; dark bodies (*pyr.b.*) in central end of cells of 4th quartette; vesicular outgrowths (*ves.*) on surface of supraequatorial cells.

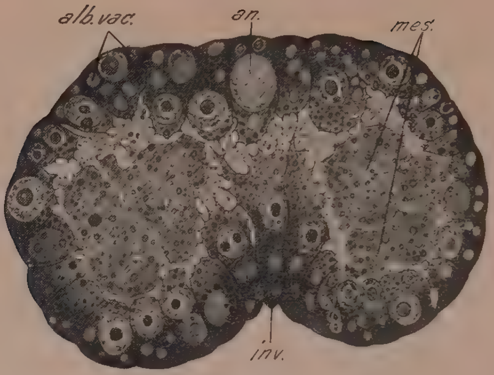

Fig. 11. Early gastrula of *Limnaea stagnalis*. Beginning invagination o archenteron (*inv*). Albumen vacuoles (*alb.vac*) in ectoplasmic part of th cells; at animal pole (*an.*) cells with giant albumen vacuoles. *mes.* = mesoderm cells.

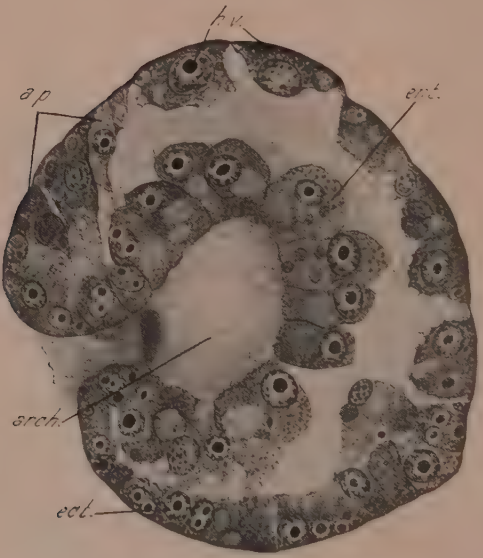

Fig. 12. Late gastrula of *Limnaea stagnalis*. Beginning of differentiation cells of head vesicle (*h.v.*) and apical plate (*a.p.*) differing from small ecto derm cells (*ect*) of other regions. Entoderm cells (*ent.*) with large albume vacuoles; albumen coagulum in archenteron (*arch*) with secretion droplet

REGULATION OF THE DENSITY OF THE INSECT-POPULATIONS IN VIRGIN-FORESTS AND CULTIVATED WOODS

BY

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1. INTRODUCTION

In literature many data may be found that point to the fact that the chances of an outbreak of an insect-plague are much smaller in a virgin-forest than in a wood influenced by men, or in plantations of plants that naturally belong to the virgin-forest. Thus SCHIMITSCHEK (1940) was able to show that, in Turkey, *Ips sexdentatus* Börn. only occurs in pure-woods planted by men, and not to any great extent in virgin-forests; SCHNEIDER (1939) found the same with regard to *Oreta carnea* Saalm., a Depranid feeding on gambir belonging to the virgin-forests of Sumatra: in gambir plantations it is necessary to spray regularly with insecticides in order to keep the crops. In the virgin-forest a gradation of this caterpillar has never been observed. The research after *Cryptorrhynchus gravis* F. showed that this beetle does not damagingly occur in virgin-forests, whereas it does in trees planted round houses at a great distance from the forest (VOÛTE 1935). EIDMANN (1942, 1943) points out that the African virgin-forests are free from insect-pests in contrast with the forests where men have interfered; FRIEDERICHS (1928) gives the same information about the virgin-forests in Oceania which he visited, VON HASSEL (1925) about those of S. America.

Many research-workers are even of opinion that in virgin-forests no plagues occur at all (see a.o. SCHIMITSCHEK (1937) who did not observe any plagues in the virgin-forests of Turkey; SCHNEIDER who comes to the conclusion that the virgin-forests of Sumatra are unsuited to the occurrence of insect-plagues; PODHORSKY (1933) who thinks that forests left to themselves only suffer from insect-pests in those cases when storm, avalanche etc. have caused damage).

Opposed to this is EIDMANN's opinion that the virgin-forests in Labrador, if they are not done away with by other causes, are destroyed by insect-pests at the moment when they have stopped growing. According to EIDMANN these plagues occur specially in "überalterten oder sonstwie besonders disponierten Bestandstypen" (p. 243). So these insects may, in a way, be regarded as secondary insects, as they can only fully develop in trees that are no longer in prime condition. In this connection I want to refer to an observation of HESSELINK (1928), according to which only trees that have stopped growing were defoliated by *Panolis flammea* Schiff. in Holland, whereas well-growing trees were left undamaged.

About the general validity of this principle in northern woods EIDMANN observes: "Die Grundlage hierfür bildet letzten Endes die sogenannte 'Katastrophentheorie', d.h. die immer mehr durchdringende Anschauung, dass der Nordische Urwald, wie er für Labrador und das übrige boreale Nordamerika charakteristisch ist, keine unveränderliche Vegetationsform darstellt, sondern in einer ständigen, in langen Zeiträumen sich wellenförmig wiederholenden Entwicklung begriffen ist, deren Wiederbeginn in der regel durch Naturkatastrophen (vor allem Waldbrände, Windbruch und Insektenkalamitäten) eingeleitet wird" (p. 231).

Similar circumstances also exist with regard to certain natural douglas-woods, and other woods as SCHENK (1924) informs us. Here the catastrophe is always caused by forest fire, resulting from a stroke of lightning.

Compared to the tropical virgin-forest, this northern wood is very poor in species. It is practically a purewood. Thus EIDMANN gives as the component parts of the wood in Labrador 60% *Picea mariana* B.S.P. and *Picea canadensis* B.S.P., 35% *Abies balsamea* Mill, 4% *Betula papyrifera* March, and 1% *Populus tremuloides*. In Siberia, too, the virgin-forest is poor in species. CAJANDER (1906, 1943) found that the virgin-forests of the North tend to impoverishment. When, after a forest-fire, a new forest begins to grow, it consists originally of several species of trees. In course of time, however, more and more species are crowded out, until eventually a wood comes into existence which may practically be regarded as a purewood. With regards to herbs the same process takes place. Opposed to this is the fact that in the Cameroons the woods contain about 800 species of trees, of which 500 or 600 belong to the predominating ones (EIDMANN 1942).

From the reports of the researchers mentioned above it may probably be concluded that, in principle, there exist two kinds of virgin-forests: *a*. virgin-forests that principally consist of trees of the same age and of a very restricted number of species, *b*. virgin-forests that are strongly mixed and consist of trees of different age-classes.

When in the latter sort of virgin-forest a tree begins to wilt, it will be attacked by an army of secondary insects which contribute to the acceleration of the process of dying. The open space thus coming free is taken up by a great number of bushes and trees, so that on that spot a rejuvenation takes place.

In the virgin-forest mentioned under *a*. all predominating trees are of about the same age. Therefore they will all show the infirmities of old age at about the same time, so that, at a given moment the whole forest is wilting. Now, this wilting forest is an easy prey to many sorts of insects so that it will be ruined by insect-pests; a new development will then begin ending in a new forest of about the same structure as the old one.

It is difficult to decide whether the forests mentioned under *a* occur specially in the north and the ones mentioned under *b* in the tropics. It is quite conceivable that transitory forests also occur in the tropics. I could, e.g., very well imagine that one species of tree naturally predominates in the long run as is the case in the ironwoods in the Netherlands East Indies according to FRIEDERICHS, and that this species does not tolerate any rejuvenation. Such a forest will eventually be ruined in the same way as the forests in Labrador described by EIDMANN. It is even not inconceivable that, in the long run, this fate lies in store for all tropic woods and all the woods of the temperate zones.

Such a natural end is, however, not contrary to the idea that there is a great stability in the virgin-forest, i.e., that the chance of the natural development of the forest being interrupted by calamities of a biotic character, is very small. It is probable that e.g. also the northern forests, not yet weakened by age, are to a considerable degree immune from insect-pests. EIDMANN reports no pests caused by indigenous insects in these stages; TRÄGÅRDH (1926) says that Swedish woods are not troubled by primary insects. In this connection it must be observed that the woods in Sweden are exploited, so that the chance of too old woods is not very great.

The lack of observations on the occurrence of insect-pests in virgin-forests, naturally does not prove that such pests never occur, but from it we may conclude that the virgin-forest effectually protects itself in a high degree against the outbreak of such pests. In this connection we are reminded of SCHNEIDER's observation that even the gambir-plantations bordering on the virgin-forest are little troubled with *Oreta*, in contrast with those plantations that are situated a long way from the virgin-forest.

In a cultivated wood the chances of an occurrence of insect-plagues are not imaginary. Many species of insects are here in a more or less labile equilibrium. In these species the density of population will generally be what I should like to call: the natural density, i.e. the density where the species is not noxious and in, be it labile, equilibrium with the surroundings. Probably this density may be compared to that in which the species also occurs in the virgin-forest. [1]) That under these circumstances a considerable part of the tree-leaves is eaten is proved by EIDMANN's observation, according to which 20 to 25% of the leaves of the African rain-wood falls a victim to the devouration of insects. From time of time, however, the insect in question strongly increases, so that a gradation sets in, generally ending in a crisis after which the species occurs in very small numbers in the area in question and only reaches the average density of the natural population after a longer or shorter interval. Examples of this are furnished by the forest-insects of which periodical plagues are known: *Diprion pini* L. (BESEMER 1942 a.o.), Black arch (ZWÖLFER

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[1]) The natural density must not be confused with NICHOLSON's „steady state", i.e. the density where host and parasite are in equilibrium. The natural density is not one level but varies between certain limits. When the steady state of the host and his monophagous parasites is calculated, it will always have to fall within the limits of the natural density. Neither may the natural density be confused with SCHWERDTFEGER's „eiserne Bestand", as, in my opinion, in an equilibrated population a density may occur which lies far above that of the „eiserne Bestand" (see p. 449).

1933 a.o.), *Panolis flammea* Schiff. (ZWÖLFER 1921 a.o.) etc.

GRAHAM (1939) reports the following characteristics in the outbreak of insect-pests: 1. extremely dense population, 2. the pests appear and disappear with great suddenness, 3. they occur in weatherconditions which are favourable to the insects, 4. generally, but not always, they occur in extensive areas; sometimes certain types of woods are attacked in practically their entire extent, 5. usually the outbreak of the pests is periodically repeated, 6. more pests occur in forests in temperate zones than in tropic ones, 7. they principally occur in woods where one species of tree predominates, 8. they occur most often in forests that should already have been cut down, and are most serious there.

These characteristics are also shown in our woods. Only, in our country the periodicity of the occurrence of the pests is not very noticeable. In Germany this periodicity is an established fact, as is shown by EIDMANN's (1931) research. In connection with point 8 HESSELINK's researches may be mentioned here. He observed that, during the great plague in the Netherlands, *Panolis* exclusively attacked trees of which the growth had practically stopped.

Of importance is GRAHAM's observation that, generally, some trees are seriously attacked, before we can speak of a plague. One or two years later the population has sufficiently increased to defoliate the whole forest. In many cases such a course of the occurrence of a plague may also be observed in our woods. I noticed it with the occurrence of *Pissodes piniphilus* Herbst (1940) where, however, the pest itself failed to come, moreover with *Diprion pini* L. (see also BESEMER) and with *Evetria buoliana* Schff. (see also LOVINK and RITSEMA BOS 1894). This phenomenon may be connected with a predilection for certain trees such as, e.g., is the case with the mango-beetle (VOÛTE 1935) or with a slight degree of susceptibility of the trees, through which, in normal years, only some of them can be attacked, e.g. *Evetria buoliana* Schff. (VOÛTE and WALENKAMP) and secundary bark-beetle of the Scots pine which can only bore themselves into wilting trees; it may also be connected with the social inclinations of the insects, as might be concluded from KANGAS' observations with regard to *Pissodes piniphilus* Herbst. He observed that imagines may strip certain trees in such a way that they are so weakened that they form a suitable residence for the larvae. In such a case the tree is covered with eggs from top to bottom.

However, there is also a possibility that in this case we have to deal, not so much with social instinct as with a predilection for certain trees.

Finally, it may depend on the reluctance of certain insects to leave the tree on which they have developed, as I was able to observe with the Citrus bug, *Rhynchocoris serratus* Don. (= R. *poseidon* Kirk.) (1935).

So the attacking of certain trees before the outbreak of the pest is connected with certain habits of the insects, or with a certain relation between insect and food-plant. If such a relation does not exist, and if the insects have no social inclinations, the plague will more uniformly develop in the wood. It is then, of course not necessary for every tree to be attacked in the same degree, because some trees are always more attractive to insects than others. In our country such a manner of attack may, e.g., be observed in *Bupalus pinarius* L.

As the climate influences populations of different densities in the same way and consequently has no regulating influence, there must be other active factors that see to it that, in the virgin-forest, and to a lesser degree also in other woods, a certain density of population is kept up which will, of course, vary within certain limits. In the area the species can maintain itself permanently, the average climate must permit a slower or quicker growth of the population. If this were not the case the species would become more and more rare and finally become extinct.

So let us suppose that the climate always permits a slow growth. If there were no other factors influencing the density of population unfavourably, it would eventually grow according to a logarithmic curve. Among the latter factors are those which possess a regularizing influence and therefore take care of the density being, in the long run, maintained at a certain level. I gave a survey of these factors (1943) to which I refer the present reader.[1]

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[1] The factors influencing a population are subdivided as follows:

AA. Factors of the first degree (influencing the population directly = R. factors).
- A. General factors (all individuals are physiologically influenced).
  - 1. Independent factors (independent of the density).
  - 2. Dependent factors (dependent on the density).
- B. Selective factors (part of the individuals are mechanically damaged).
  - 1. Independent factors.
    - a. Insatiate factors (with the augmentation of the density, this

This regularizing influence is most beautifully shown by PEARL and his collaborators. He pointed out that a population of *Drosophila* cultivated in a closed space with a superabundance of food, grows up to a certain level and maintains itself there. On this level the internal resistance is such that a further growth is out of the question. PEARL (1925) showed that a population of men also increases according to this curve, which he takes to be a logistic one. The existence of such a curve has also been proved to exist with regard to other species of animals: *Tribolium* (PARK, VOÛTE), *Calandra* (MACLAGAN, VOÛTE) etc.

These observations could be done best with regard to stored-products-insects that could easily be cultivated in a closed space in the laboratory. In the open air there are always a great number of factors whose influence cannot be determined, and which may not inconsiderably influence the character of the curve. Thus, e.g., insects can, in the open air, always emigrate. That this characteristic is of great importance may be shown in *Calandra oryzae* L. (VOÛTE 1937/38). The difference in growth between two populations of *Ageniaspis* sp., parasites of *Phyllocnistis citrella* Staint. on shaded and unshaded citrusplants, may be pointed out in this connection. On the shaded plants the density increased in accordance with a curve showing some resemblance to that of PEARL. On the unshaded plants the population grew in an entirely different way (VOÛTE 1935).

The question whether this curve is indeed a logistic one or some other S-shaped curve will not be further entered into (see FELLER (1939) and MARTINOTTI (1932)). This S-shaped curve represents the natural growth of a population, only impeded by endogenous factors. In NICHOLSON's opinion the increase of this inner resistance is caused by "competition". This may be competition in the matter of suitable residences, food, oviposition, milieu, etc. In this case it may be mathematically calculated how this "competition" will increase with the increasing density of population.

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factor is never, or not soon saturated).
b. Satiate factors (the factor is soon saturated).
2. dependent factors.
3. Modifiable factors (factors which, in their development are dependent on the density, e.g. monophagous parasites).
BB. Factors of the second degree (influencing the R. factors).
CC. Factors of the third degree (influencing those of the second degree) etc.

2. GENERAL SCHEME OF THE GROWTH OF A POPULATION AND OF THE INFLUENCE OF THE RESISTANT FACTORS ON THIS GROWTH

Let us now start from a forest-insect which, as the result of some circumstance or other, occurs in numbers far below the average of the natural density. This population will try to grow according to the S-shaped curve mentioned above. At first the dependent factors [1]) to which the endogenous factors belong as well, will not exercise any influence. The modifiable factors [1]) do not play an important part either, as the density lies below the critical level indicated by SCHNEIDER, and these factors will only develop above this level. So it are only the independent factors [1]) that oppose the increase of the insect.

Let us suppose that the insect's capacity to increase is so great that the population grows, notwithstanding the opposition of the independent factors. If this were not the case the species would not be able to maintain itself in the surroundings in question. The activity of the general independent factors [1]) remains the same, the selective independent factors remain so too, at first. The latter consist chiefly of polyphagous parasites and predators. Under natural circumstances they can always devour, or lay their eggs on, a few more prey than they have an opportunity of doing. Now, if the density of one species of prey increases, the total number of prey at their disposal increases as well. Of these a slightly larger number will be rendered innocuous. Among the prey the percentage of the insect in question has augmented a little. The consequence of this is that an identical percentage will be killed by these parasites or predators.

If the population grows further it runs the risk of certain predators or parasites specialising on the species in question. This will especially be the case when the animals are not distributed equally over the area but occur in some places in greater numbers than in others, as a result of, e.g., the way of depositing the eggs, or because in a mixed wood the trees on which the insect in question lives are scattered and do not occur in close formations. It is, e.g., a wellknown fact that birds often go back to places where they found running some time ago an easy prey.

NICHOLSON mentions this characteristic as a means to make the fluctuations in these population-oscillations less serious: "C. 84. Certain predators birds e.g. tend to concentrate attention upon those parts of the environment in which prey are abundant, and so tend to damp fluctuations in the densities of their prey".

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[1]) See note p. 440.

A beautiful example of this relative strengthening of an independent factor is furnished by the mortality among the larvae of *Pissodes piniphilus* Herbst as a consequence of the feeding of woodpeckers. As KANGAS (1938) already observed these beetles are inclined to attack the trees in groups and cover them with eggs. In such a tree a great number of larvae may subsequently be found. I was able to observe that of such groups more than 95% was eaten by woodpeckers, whereas of the larvae not living in groups only about 5% was destroyed. Very interesting in this regard is the research of ENGEL (1942) executed within the scope of the important *Bupalus*-research of the Institut für Waldschutz in Eberswalde. ENGEL found that predators – birds, boars etc. – concentrated their attention almost exclusively on insects occurring in masses. In this connection he says: "Der eigentliche kritische Augenblick, in dem die Populationskurve eines Insekts aus einem reinen und einem gemischten Bestande sich in ihrer Amplitude zu unterscheiden beginnen fällt vielleicht . . . mit dem überschreiten des 'eisernen Bestandes' zusammen".

In this connection I may be permitted to refer to FRANSEN's observation; he saw that colonies of caterpillars of the brown tail moth, which he put out in an area where they did not otherwise occur, were very soon destroyed. Probably this was done by birds which had specialised on such colonies. Digger-wasps too often behave in this way, i.e., they like to hunt in surroundings where they are sure of finding numerous prey. I myself have been able to observe that a colony of lackey-moths which had been discovered by a red ant (*Formica rufa* L.), was attacked and entirely destroyed by these ants.

The consequence of this specialization is that the activity of the independent selective factors, although their absolute strength does not vary, increases with regard to the species in question.

If the critical level (SCHNEIDER) is passed, modifiable factors, mostly monophagous parasites and predators may increase in intensity as well. For this see the classification of the resistant factors given by me, and the publications of SCHNEIDER (1939) and SMITH (1935). Originally the activity of these factors is very slight, the longer the density of population remains over the critical level, and the farther it surpasses this, the more powerful these factors become.

Here it may be observed that the development of the modifiable factors is stimulated by the above discussed inclination of many insects not to spread evenly through the wood, but to occur in great numbers in some trees and not at all in others. In this way the critical density is far surpassed in some places, whereas, taken as an average over the whole of the wood, it has not yet been reached. The result of this is that many of these small groups are destroyed by their monophagous parasites. As a result of this circumstance the monophagous parasites can maintain themselves on a higher level than would be the case with a more equal distribution of their hosts. NICHOLSON pointed out this fact as a possibility to keep the plague permanently in check by its monophagous parasites.

As a result of the circumstances mentioned above, the resistance of the surrounding increases and it will depend on the rapidity of the growth of the population whether it will increase still farther or will again decrease in strength. In this case, parasites and predators lose their special adjustment to the species more and more. So the circumstances have again become such that a slow increase of the population becomes possible.

Sphinx pinastri L. is a species which, according to GÖSSWALD (1936), is completely kept in check by its parasites and predators. With regard to this species we must suppose that the density is more or less regulated in the way discussed above, the more so as this insect is highly unsusceptible to the influence of the climate. The same holds good for *Oreta carnea* Saalm. in virgin-forests. SCHNEIDER was able to analyze the activity of the resistant factors for this insect, for the greater part.

TOTHILL's research (1923) gives a beautiful instance of the regulating action of these factors. He observed that *Cacoecia fumiferana* Clemens (the spruce budworm) which was on the point of developing into a plague was checked by parasites and predators. Birds ate 38%, parasites 60% of the caterpillars. In this case the structure of the wood only allowed of a slow increase of the population.

If the density increases in spite of the greater resistance, the satiate independent selective factors lose strength with regard to the species. FRANSEN could prove this for the influence of birds on the winter nests of the brown-tail moth. Where the density of this moth was great, and many winternests could, consequently, be found, the percentage of cleaned-out nests was low. If there were only few winternests, they were often all more or less picked clean.

Tothill (1922) observed pratically the same thing with regard to the influence of birds on the populations of *Hyphantria cunea* Drury (the fall webworm). I append his data:

year	1912	1913	1914	1915	1916	1917	1918
number of nests on 80 m of road	100	20	3	2	2	5	30
% eaten by birds	9	53	87	88	90	74	73

As a result of this decreased resistance the population can again increase more rapidly.

In connection with this decrease of the resistance of the surroundings after the population has risen above its natural density, so with the fact that the population has, so to say, escaped from its resistant factors, I should like to call this phase which follows that of the natural density, the "escape-phase".

As the density increases further the dependent factors, selective as well as general, which originally did not exist or were of little importance, will increase. These factors have a tendency to maintain the density at a fixed, high level. So they effect a growth which continually decreases as the density increases. Moreover, the circumstances become more and more favourable for the modifiable factors, so that they become more powerful. Examples of this may be found in the rise of parasitism by monophagous insects during gradations of several of our wood-pests and enemies of our agricultural and horticultural plants. In this connection *Achrysocharella ruforum* Krausse may again be mentioned, the egg-parasite of *Diprion pini* L., which can infect as much as 100% of the eggs during a gradation (Besemer). Also many other sorts of egg-parasites (Smirnov and Wladimirw; see Smith), the parasite of the white louse of the sugar cane, *Encarsia flavoscutellum* Ashm. (Hazelhoff 1928), *Ageniaspis*, parasite of *Phyllocnistis citrella* Staint., which may parasitize up to 100% of the caterpillars (Voûte), etc.

Eventually these factors become so strong that they cause a fall in the density of population. In some cases it is shortage of food, in others shortage of food combined with modifiable factors. It occurs very often that only shortage of food causes the crisis. It is always observed where woods have been cropped quite bare.

The black-arch-plague on the Rominther Heide affords a good example of case where the two groups of factors cooperate (NIKLAS 1939). In this case the animals were enfeebled as a result of overpopulation and shortage of food, thus becoming susceptible to illness in the middle of the plague-territory. The monophagous parasite *Parasetigena segregata* Rond. then went to the periphery where it destroyed the less numerous but healthy caterpillars.

Another instance is given by TOTHILL (1923): during a plague of *Cacoecia fumiferana* Clemens (the spruce budworm) 50% of the caterpillars starved to death and 11% was killed by storm. After that the rate of mortality suddenly increased as a result of the activity of parasites and predators, to such a degree that the plague was over.

Instances where the crisis was caused by modifiable factors are furnished by the above mentioned *Ageniaspis*, *Achrysocharella*, and *Encarsia*.

In this connection we want to mention SUBKLEW's (1939) important research-work who, from his own observations and those of SCHWERDTFEGER reached the following conclusion: "In allen Fällen stimmen diese kausalen Bevölkerungsanalysen darin überein, dass die Massenvermehrung der Schädlinge allein durch biotische Faktoren der verschiedensten Art bei wechselnden Wirkungsgrad beendet wurde".

So here, too, the modifiable factors are of the greatest importance.

This latter phase I should like to call "the crisis".

The density of population before the crisis depends on the rapidity of the development of the species and the character of the resistance-factors. If they allow a slow growth, it will be possible for the modifiable factors to have a considerable strength already at the beginning of the escape-phase, so that they can cause the crisis to manifest itself soon. In a rapid growth of the population the modifiable factors will need longer to check the gradation, which will by that time have reached much more serious proportions. This is not in conflict with the fact that SCHWERDTFEGER could show, from researches after the population movements of *Bupalus* and *Panolis* in Scots pine woods, that, during a plague, the density is in the first place determined by the number of years during which a population is growing, and only in the second place by the rapidity of its growth. For, when the process of growing lasts for a long time, this only means that the resistant factors have, for a long time, not been able to keep the species in check and these factors may for the greater part be abiotic factors.

As NICHOLSON shows, the degree to which the resistance-factors reduce the density, depends on the force of these modifiable factors during the crisis; in its turn this force depends on the density of population at that moment. So, the denser the population before the crisis, the stronger the modifiable factors must be to cause a crisis, the shorter this crisis lasts, and the smaller the density when the crisis is past. That this is not only a theory but an established fact is proved by SCHWERDTFEGER's (1935) and ENGEL's researches after the gradation-movements of *Bupalus* and *Panolis*, mentioned above.

So different groups of resistant factors exert their influence during different phases.

The independent general factors (climate, chemical character of milieu, sort of food) always exert the same influence in the different phases, mentioned above. In this connection it may be observed that an increase of the dependent general factors – e.g., famine – may weaken the insects to such a degree that they have less resistance against the independent factors of the same group (see also HOFFMANN 1933).

Of the selective factors it is especially the independent that are of importance in the phase of natural density. The dependent factors play no part when the density is so low. The modifiable factors only play a part when the density has for a long time surpassed the critical level. If this is not the case, no great value need be attached to their importance.

In the escape-phase the importance of the independent satiate factors of the selective group decrease rapidly. If the density increases very much, the importance of the insatiate factors decreases, because here, too, a relative level of satiety occurs. As an example EIDMANN's observation may be mentioned, according to whom the area dominated by a colony of *Formica rufa* becomes smaller during a plague.

During this phase the importance of the modifiable and of the dependent factors increases.

During a crisis especially the modifiable and the dependent factors are of importance.

In connection with the above we may be allowed to point to the comparatively slight value of a parasite-analysis that has been undertaken once only as is so often the case. For, if the analysis takes place during or a short time before a crisis, a very unfavourable impression will be obtained with regard to the parasites, which belong to the independent factors, and may also be responsible for the fact, in general the species does not proceed to a gradation. If the analysis is made during a phase of natural density, no reliable picture is obtained of the part acted by the monophagous parasites, which belong to the modifiable factors. BESEMER's research may serve as an instance of this. His first parasite-analysis was undertaken when the population of *Diprion pini* L. already found itself in the escape-phase, and did not furnish a single specimen of the so important egg-parasite *Achrysocharella ruforum* Krausse. Two years later the analysis produced a parasite-percentage by this species of almost 100%.

The three phases mentioned cannot be sharply divided. In the first phase the population is balanced, kept in check by the resistance factors. In the escape-phase this balance is upset. In what density this balance still exists and when exactly it commences to be upset, cannot always be ascertained, so that the limit between these two phases cannot be exactly fixed either. The crisis is characterised by the rapid relapse of the density, sometimes to an extremely low level. As has been said, NICHOLSON showed that this level, when the crisis is caused by parasites, will be lower proportionately as it was higher before the crisis.

3. REGULATION OF THE DENSITY OF POPULATION IN THE SCHEME

Under regulating factors I understand those factors which help to keep the density of population at a certain level.

In the above-mentioned scheme of a gradation, two moments may be observed when the resistance factors have a regulating action: A. at the topmost limit of the phase of the natural population and B. at the topmost limit of the escape-phase.

A. The regulating action is in the first place caused by the independent selective factors (polyphagous parasites and predators), many of which, as has already been observed above, have the power to specialize on the species in question, and have, moreover, certain reserves of strength that are not used normally. These factors form an important and, at first, increasing check on the growth of the population. The greater the possibility of increase of this check, the more is the growth of the population slowed down. This will give the modifiable factors (monophagous parasites), whose critical level must lie within the zone of the natural density, time to develop. This will again strengthen the check. Birds moving about in droves, which are attracted and held by the high insect population, must also be counted among these modifiable factors. The density of population where the regulating forces manifest themselves forms an integral part of the natural density. According to ENGEL, SCHWERDTFEGER'S collaborator, these factors become active when the density of population has surpassed that of the "eiserne Bestand". For this reason "eiserne Bestand', and natural density are not synonymous. For the same reason the terminology adopted by SCHWERDTFEGER for the development of a gradation does not fit my scheme.

B. In the escape-phase it is in the first place the dependent factors that have a regulating action. They, however, either regulate the density at a high level (see the researches of PEARL 1925, MACLAGAN 1936, VOÛTE 1937/38 a.o.) or they make the population decrease very much through food-shortage. By the side of this the modifiable factors are active, causing a crisis, and often reducing the density to an extremely low level.

In theory it is possible that the density of a population is kept at a low level exclusively by the activity of parasites and predators belonging to the modifiable factors. In general these parasites and predators will be monophagous. At the critical level of the density of population of their host their number will neither decrease nor increase. Now when, at this critical level, the number of parasites is so high that the hostpopulation cannot increase either, or that its density decreases, a state has developed where host and parasite or predator balance each other. NICHOLSON calls this the "steady state". When, however, a slight deviation from this state occurs, then – supposing that host and parasite influence each other exclusively – oscillations will occur in the density of population of both, tending to increase in amplitude until a crisis is reached, with the result that the host population no longer forms a coherent whole. After this the density of the parasite will also decrease to an extremely low level (NICHOLSON).

Polyphagous parasites may, theoretically, have the power to control their host permanently, at least when more than one species of host is available at the same time. This follows from

NICHOLSON's research. He comes to the following conclusion: "C. 42. When a parasite attacks other host species in addition to the one it controls, interspecific oscillation is reduced in violence and its amplitude is likely to decrease in time". This is a result of the fact that, thanks to the presence of other hosts the density of a parasite after a crisis never becomes so extremely low as is the cause with monophagous parasites. In practice many cases where a successful biological control has been applied may serve as examples of such a regulation by a polyphagous parasite, occurring as a modifiable factor. I mention here the destruction of *Levuana iridescens* Beth-Baker by means of the Tachinids fly, *Ptychomyia rimota* Ald. After its introduction on the Fiji isles this fly caused a crisis in the *Levuana* caterpillars which occurred there in masses, through which the density of the latter was practically reduced to 0 (TOTHILL, TAYLOR & PAYNE 1930). Later it appeared that the density of the flies had not been reduced to 0 from which it may be concluded that it was able to maintain itself on other hosts. SWEETMAN (1936) gives a series of other examples, where noxious insects are permanently controlled by the introduction of polyphagous parasites.

NICHOLSON shows that the proportion prey-predator gives less occasion to the occurrence of oscillations in the density than that of parasite-host: "C. 52. In general, predators and their prey should tend to be maintained at their steady densities, for increasing oscillation is unlikely to be produced between predator and prey".

Polyphagous predators with cannibalistic tendencies, behaving as a modifiable factor with regard to a species, may maintain themselves on a much higher level after a crisis as a consequence of their cannibalism, thus preventing a very high density of their host. This means that the crisis will be less serious too. The same holds good, be it to a lesser degree, for the other polyphagous predators that can maintain themselves at a higher level during a crisis, at the cost of other prey. Such predators are sometimes able to keep the population of their prey at a permanent low level. That this is possible in theory, is shown by NICHOLSON. In practice we find many instances, e.g. *Rodolia cardinalis* (Muls.), predator of *Icerya purchasi* Mash. etc. (SWEETMAN).

Another example of this is furnished by the balance between lions and their prey in the Kruger Park in South Africa. Very slow oscillations occur. If the number of prey decreases too much as a result of a too great number of lions, many young lions weaken and die, so that their density of population decreases. In the same way the density of the lynx (*Lynx canadensis* Keer.) is regulated by that of its prey, a hare (*Lepus americanus* Eral.) (cf. Low 1895). The regulation of the density of the hare is not exclusively effected by the lynx, but also by an illness which often decimates their numbers.

When an animal is exclusively regulated by a predator, this means that the species in question will exist as long as the predator is active. This is the case with the lions and their prey, the lynx and the hare, etc. In the African forest described by Eidmann, with its equable temperature, no sharply divided generations are found, and no periods when certain insects have disappeared. So any insect-eater may here act as a modifiable factor, which according to Nicholson's calculations contributes to making the oscillations in the density of its host smaller. The more so when we have to do with polyphagous predators which, according to Nicholson, counteract the oscillations in the density of population to an even stronger degree. The extremely equable climate itself will not cause oscillations. It is self-evident that, if anywhere, a great stability reigns in such a forest.

In connection with this a single word may be said about the scarcity of *Ichneumonids* observed by Eidmann in these forests. When the predators regulate the species in the same absolute way as in the African forest, i.e. when such a large proportion of the insects is eaten, the parasites get an extremely small chance to develop, because as we saw, they are eaten together with their hosts.

In the virgin-forests of the temperate zones entirely different conditions prevail. Here most insects are only active during a few months, and the long-lived predators must depend on a whole series of prey, belonging to different species.

4. INFLUENCE OF THE CLIMATE ON THE COURSE OF THE SCHEME-DEVELOPMENT

In this paper it has been presupposed that the climate is equable. In temperate zones this is, however, not the case, so that we must trace the influence climatic oscillations have on the scheme mentioned above. In the following chapter general climatic factors are exclusively taken into account; climatic factors influencing the animals physiologically, and the total of these factors will be considered as one whole.

Nicholson treats the theoretically possible influence of the climate on the proportion host-parasite. He comes to the conclusion that regular climatic oscillations cause regular oscillations in the density of population. If the climatic oscillations are irregular, the density oscillations are irregular too.

Such regular climatic oscillations will, e.g., be found in countries where a wet and a dry season alternate. In our country the oscillations are, as a rule, very irregular.

Climatic conditions favourable to the species, mean a decrease of the independent resistance-factors, so, at first, an increase of the population. Whether this increase will take the population as far as the escape-phase depends on the degree of auspiciousness of the climate and the extent of the regulating action of the polyphagous parasites and predators. If the density reaches the escape-phase, increase is a matter of course, ending eventually in a crisis.

So it goes without saying that there exists a close connection between the climate and the outbreak of insect-pests. Observations on such a connection have been made with regard to the black arch (Knoche 1932, Zwölfer 1933), *Dentroctonus* (Keen 1937) and many other insects. The very important researches of Schwerdtfeger (1935) may in particular be pointed out in this connection. In most cases the movements of one insect species show a high degree of concurrence, only with *Dendrolimus* this was not the case, although in this insect, too, the capacity to increase in the different woods during different years, shows many similar traits, as is shown by the graphs he published. One thing and another strongly point to a climatic influence.

The Mango-beetle which occurs in great numbers in moist Western Java and is practically non-existent in eastern Java, only occurs to a damaging degree in Cheribon in wet years. It is a well-known fact that the young beetles cannot resist the drought when they have just left the fruit. A certain periodicity may even be observed in the occurrence of certain pests, connected with solar spots (Eidmann). The solar spots influence the climate, and the climate influences the pests.

In the Netherlands plagues are often seen to occur after a cold winter and a warm, dry spring. Whether this cold winter influences the insects directly of indirectly must, as yet, be looked into.

If the weather changes after the escape-phase has already been reached, the growth of the population is, of course, checked. The character of the change of climate will decide whether the population will continue to grow or be brought back to a lower level. In our country the climate alone is able to bring a pest to a standstill.

The climate can also show its influence indirectly, by promoting or checking parasites or predators. Thus it may be observed on Java that a scale insect-pest on *Citrus* was ended by the appearance of a parasitical fungus immediately after the rains had set in (VOÛTE 1935). For other instances the reader is referred to par. 7.

In general it may be said that great climatic oscillations impede the stability of biocoenosis. From this it may, however, not be concluded that insect-pests are always more serious in such a climate than in an equable one, which, in its averages, is equal to the first. For the climatic oscillations are not only able to disturb the balance and so cause a pest to break out, they can as well check a pest that has already broken out. If, in any equable climate the balance has been disturbed, thus enabling an insect to develop into a pest, the climate will not have much influence on the course of its development.

Theoretically insects whose balance is not very stabile, will sooner lose this balance in a non-equable climate than in an equable one. This is probably one of the reasons why the tropic forests suffer much less from pests than those of the temperate zones (GRAHAM).

In the warm, moist and rather equable climate of many tropical regions, the resistance offered by the climate against the occurrence of insect pests is, however, not very great. BODENHEIMER's (1928) idea, according to which few insect-pests occur in the tropics as a result of the great distance between vital- and development-optimum in the tropical insects, is not exact, considering the great number of insect-pests in agricultural and horticultural plants.

How violent, and especially how lasting a plague of tropical insects may be, appears from LEEFMANS' research of *Brachartona* (1928), *Oryctes* (1920), *Stephanoderes hampei* Ferr. (1923, '24), *Helopeltis* (1917), the coconut locusts (1927) etc.; VAN DER GOOT's of the rice borer (1925), the scale insects (1915) etc.; VAN DER VECHT's of the pepper bug (1933); KALSHOVEN's of the teak termite (1930); BETREM's of the shothole-borer (1930, '31, '32); PAGDEN's of divers noxious fruit-insects (1931). EIDMANN says that, in Africa, the woods where man has disturbed the balance, often suffer severely from insect-pests. See also JANISCH's research (1930) on the development of *Prodenia*, which insect can, under certain circumstances, multiply very rapidly. How rapid the increase of certain planteaters may be, became evident to me during my research of the Citrus mite which makes the fruit appear to be powdered with dust in a few weeks (VOÛTE and ZEILINGA 1934/35).

The more extreme the climate becomes, the stronger its action as a resistance-factor and the smaller the chance the population gets of reaching the escape-phase. In connection with this TRÄGÅRDH's explanation is of importance. He says that the primary wood insects are of small importance in Sweden because they are kept in check by the rough climate. PROSOROV (1929) observed the same in the cold regions of Siberia.

From the above it may be concluded that only an extreme climate is directly capable of preventing gradation. In such a climate it only occurs when the conditions appear which make the northern woods non-permanent ones. In the tropics as well as in the temperate zones the climate allows the possibility of the occurrence of gradation. That in the woods of countries with an equable climate the insect-pests are often more numerous and more violent than in the tropics, as is evident from literature (see also GRAHAM) is a result of the fact that oscillations in the climate may easily lead to a population's balance being upset. The occurrence of the teak caterpillar on Java and in India proves, however, that also in the tropics pure forests are in no way secure from defoliation.

5. TRANSITION FROM VIRGIN-FOREST TO CULTIVATED WOOD AND ITS INFLUENCE ON THE FAUNISTIC POPULATION

What the virgin-forests in the Netherlands have looked like, we can only approximately say. Where there still are virgin-forests in Europe or anywhere else, they have been extremely summarily examined as a living-community. EIDMANN gives an interesting ecological analysis of the african rainwood. He describes the overwhelming wealth of plants and animals. The number of insects is so great that 20–25% of the leaves is devoured. An army of insectivores and only few parasites live on these insects. The density of the insects is very well regulated.

Insect-plagues never occur. It is a striking fact that, with regard to mammals and birds, predators play an extremely inferior part as a regulating factor. The density of the fruit-eating mammals and birds will probable be principally regulated by the quantity of food, illness, etc. In my opinion the part played by the latter must not be underrated, e.g., combined with a temporary shortage of food. Plant sociology teaches us to imagine what our european virgin-forests may have looked like, i.e., of what elements they must have been composed. In considering the lists of plants compiled for the climax-forests in our country by this branch of our biological science, we are immediately struck by the fact that these forests must have been very mixed. They possessed well-developed layers of bushes and herbs consisting of many species. Compared to this wood, practically all cultivated woods are very much impoverished. It is true that exotics have often been imported but they generally took the place of native plants, so that they were not really an enrichment. An enrichment occasionally takes place. Thus, e.g., the presence of *Prunus serotina* and perhaps also *Amelanchier canadensis* may be regarded as an enrichment of our oak-birch woods. Our researches have, however, not yet been sufficient to form a well-founded opinion in this regard. Our cultivated woods are generally pure growths, without much, or with very little undergrowth. Of late it has been tried to improve this by undersowing the monopinewoods with hardwood. Then a layer of brushwood develops, but no, or a very thin layer of herbs, so that these woods, too, remain poor compared to the native virgin-forest.

In his afforestation-scheme for the national park "de Hoge Veluwe" E. D. VAN DISSEL (1940) proposed to undersow the pine woods principally with those plants that are at home in our natural wood, possibly supplemented by *Prunus serotina* and shadbush, *Amelanchier canadensis*. Here we have to deal with an instance of afforestation deliberately reaching back to the virgin-forest, naturally in combination with the production wood, which a cultivated wood must always be.

Every native tree or plant possesses its own damagers. A great variety of trees and plants means a great variety of these damagers. Moreover there are many phytophagous animals which are polyphagous on plants. In this connection I am only thinking of insects such as the black arch etc., but also of larger animals, such as deer, does, hares etc. Each herbivore has its own specific enemies, monophagous parasites and predators. The wood is moreover inhabited by an army of polyphagous carnivores. From these facts it may be concluded that the faunistic community in the virgin-forest must have been rich in species.

From the list of plants from the Querceto-carpinetum given by MELTZER and WESTHOFF (1942) it is evident that this wood contains flowering plants practically the whole year round. The result is that insects living on honey: bees, drones, wasps, diggerwasps, ichneumonids, etc., have plenty of food during the whole year.

If the wood is made into a cultivated one, thus strongly impoverishing its floristic structure, this means that a great number of herbivores will have no means of existence. Their monophagous enemies disappear as well, and for many polyphagous enemies conditions become so unfavourable that they become extinct. Paucity of flowering plants drives the bees away from our woods. According to SCHOTMAN's handbook (1942), the gathering of honey was, in former times, one of the sources of income from our woods. Now this trade has completely disappeared from the european forests, a typical indication of the paucity of bees prevalent in our woods.

This lack of flowers is not only fatal for bees, but also for many species of ichneumonids and digger-wasps. On what must the ichneumonids live in our pine-woods without undergrowth, they who lay their eggs in caterpillars and feed on nectar? In some cases the honey-dew of tree-lice forms a surrogate, but this is not nearly of the same composition as flower-honey to which these animals are adapted.

A single thing may be said here about the litter-fauna. In our virgin-forests probably a luxuriant litter-fauna was to be found. In the cultivated woods this, too, has much impoverished in many cases. As elements of the litter-fauna live freely in the wood – flies, many beetles, etc. – an elimination of these insects means an impoverishment of the overground population of the forest.

Finally a single word may be said about the influence of the exotics on the faunistic population of the woods.

Most exotics have been introduced without their enemies, and even if this is not the case – douglas woolly aphis – at any rate without the parasites of these enemies. For this reason they cannot help in the enrichment of the fauna. On the contrary, if they take the place of native trees or shrubs in a wood, this means decreased possibilities of development to the fauna. The researches of QUISPEL (1941) and the WESTHOFFS (1942) after the influence of different growths on the population of ants in our woods, clearly show that exotics impoverish this population.

Resuming we can say that, in consequence of its floristic impoverishment and the presence of exotics, our cultivated woods are, faunistically, considerably poorer than the virgin-forests of these regions. This impoverishment not only comprises herbivorous insects and their specific enemies, but also insects which are entirely dependent on honey for their livelyhood.

6. 'IMPORTANCE OF THE FAUNISTIC IMPOVERISHMENT FOR THE STABILITY OF THE POPULATION

As has already been said in the Introduction, few or no insect-plagues occur in the virgin-forests, i.e. the escape phase is lacking. It only occurs in secondary insects. This is a consequence of the fact that a dying tree attracts insects from a great distance, so that a very strong population develops on the spot. Parasites and predators characteristic of secondary insects – e.g., bark-beetles – develop later. Generally they do not cause a crisis as the tree in question has already before that time become uninhabitable for the insects. SCHIMITSCHEK (1937) wrote about the activity of such insects in a virgin-forest. That, e.g., the pinebeetle, *Myelophylus piniperda* L., need not proceed to mass-increase in less favourable possibilities of development, and increases in much the same way as other insects, may be read from the publications of HANSON who found that, not only can thin trunks be left lying about in the wood without danger of the occurrence of these insects, but that this may even be called a useful practice, because in this way great numbers of parasites and predators are maintained.

The lack of the escape-phase in many primary forest-pests occurring in cultivated woods and causing great damage there but not in virgin-forests, points to a strong power of regulation of the R-factors which were discussed in par. 3. These factors must command great reserves of strength, and, as these reserves are bound to certain limits for each parasite and predator, a great number of these polyphagous parasites and predators.

As the question is here about polyphagous parasites and predators we must, first of all, trace whether an impoverishment of species of herbivores must necessarily be followed by decrease of polyphagous parasites and predators.

In the first place, circumstances will become more difficult for those animals which also need honey for their subsistence.

Thus Dr. BAERENDS pointed out to me an accumulation of digger-wasps in the immediate surroundings of a long-flowering Rhamnus frangula, in a region where, for the rest, very few flowering plants were to be found.

But also the polyphagous enemies of our forest-insects, which do not feed on honey, or are able to find this food at a great distance, have to overcome greater difficulties in impoverished woods than in virgin-forests.

From the observations of SCHNEIDER and others, cited above, it may be concluded that in the proportion insect-monophagous enemy there is a critical level in the population, above which the enemy will increase in number. So the modifiable factors, including the monophagous enemies, always have a tendency to force the insects below this level. An impoverishment of the wood, and the accompanying increase of the number of trees of one species need not necessarily be followed by an increase in the number of herbivores belonging to this tree. So the total number of individual insects becomes smaller if, at least, we are justified in supposing that the hunting ground is not restricted to one tree. If their hunting-ground is restricted to one tree the parasites do not keep the density of a whole wood at a certain level, but that of one tree.

As SCHNEIDER already indicates, a similar proportion holds for a polyphagous carnivore with regard to its combined prey as for the monophagous one with regard to its specific prey. In other words, there will be a critical number of prey above which the carnivorous animal can increase, and below which it will decrease in number. This critical level will be far above that of the monophagous animals as these latter are better adapted to the habits of their prey.

Now when the number of herbivores diminishes, their total will, after some time, drop below the critical level of the polyphagous carnivores. The latter have the power to push the critical level even lower by eliminating competitors. This will partly be done actively, because many insectivores not only feed on herbivores, but also on other carnivores. Those species for which the conditions of life are least favourable in the wood in question, will become extinct, thus leaving a greater number of prey for the competing species. The result of this is that, in the impoverished wood, fewer polyphagous carnivores, belonging to a smaller number of species, will be able to maintain themselves.

To this is added the fact that many polyphagous carnivores need a succession of prey to hold their own. In a wood rich in such prey it may be supposed that food for these carnivores is to be found the whole year round. If the wood impoverishes there is a chance that, during a certain part of the year few phytophagous animals will be present, which considerably decreases the possibility of existence of the carnivores, unless they are able to feed on congeners or other carnivores. OUDEMANS (1932) points this out in connection with the possibility of maintaining a good average of birds in the woods. To reach this end, he says, not only drinkable water and nesting places must be furnished, but also food. In woods where there are no plants that feed a great number of insects, the chance that insect-eating birds will not be able to hold their own in seasons that the insects are scarce, is very great.

Researches point to the fact that the carnivorous fauna has indeed become poorer in pure woods than in those woods that approach our virgin-forests. Thus TINBERGEN was able to prove that mixed woods are richer in birds, individuals as well as species, than, e.g., our pure Scots-pine woods. ENGEL too points out this phenomenon: in mixed woods the bird-fauna was richer than in a pure wood. During a caterpillar-plague, however, groups of wandering birds occurred in the pure wood, giving it a greater richness in birds. QUISPEL and the WESTHOFFS observed that the ant-fauna of our pure Scots-pine woods, beech- and sprucewoods etc. was poorer than that of the mixed oakwoods belonging to this region. The same held good for red oakwoods and Scots-pine woods with an underplanting of exotics, whereas a Scots-pine wood with an underplanting of native plants on the contrary abounded in ants. In connection with this it must be noted that, as appears from WESTHOFF's research, our native Querceto-carpinetum is poor in ants, which avoid damp, dark woods, so that only woods with an equal perviousness to light must be compared with each other.

A proof of the exactitude of the opinion stated above is furnished by observations of SHELLFORD and others, according to which different types of forests have a fauna of their own.

What is now the result of this impoverishment of carnivores? The reserves of strength which these carnivores possess as a resistance factor, decrease strongly. Thus the point on which the regulating activity in the natural density of population rests, is weakened, with the result that, during favourable weather-conditions the chance for phytophagous insects to reach the escapephase, is increased. If this is the case, a gradation will occur if the favourable weather holds.

The more the wood impoverishes the greater the chance of the occurrence of a gradation. Numerous observations point to this not only being so in theory.

In Alsatia *Tortrix rufimitrana* H.-S. and *T. murinana* Hb. are often noxious in pure sprucewoods, in mixed woods their damage is negligible (BARBEY 1931).

Pissodes strobi Peck. is only noxious in pure woods. In mixed woods the beetle is of secondary importance (GRAHAM). In Turkey *Ips sexdentatus* Börn. is, according to SCHIMITSCHEK, one of the most important enemies of the spruce. In the virgin-forest there is no question of this beetle being so noxious.

According to GRAHAM *Ellopia fiscillaria* Guen. (the "hemlock-looper") and even the polyphagous *Malacosoma neustria* L. (the "forest tent caterpillar") are, in America, noxious in pure woods only. In mixed woods they occur, it is true, but are not noxious.

It is a well-known fact that certain woods are, as it were, predisposed for the occurrence of pests. Examples of this are, in our country e.g., Bunter wood in the national park "De Hoge Veluwe" which was infested by the black arch in ± 1920, and by *Diprion pini* L. in 1938. The latter pest entirely wrecked the wood (BESEMER, FRANSEN (1938)). The woods near Drieebrgen, which suffered much from *Panolis flammea* Schiff. in 1919, were severely infested by *Diprion pini* L. in 1939.

It goes without saying that even in much impoverished woods many species of insects live in a state of equilibrium. As an example *Sphinx pinastri* L. may be cited, which is completely kept in check by its enemies. It never occurs as a plague even in the poorest pure scots-pine wood although its egg production is high, and it is, according to GÖSSWALD, quite proof against our changeable climate.

The rupture of the equilibrium in the wood may show in two ways: 1. There are no modifiable factors able to cause a crisis, or they are not effective. The species maintains itself on a high level until the population is reduced to a lower level as a result of climatic conditions. Instances of this are furnished by the brown-tail moth which ravaged the avenues and woodwalls of Northern Brabant for years and years and suddenly disappeared in 1941, probably as a result of climatological influences (VOÛTE 1942); *Tortrix viridana* L. which may be a serious pest for oak-woods for years together and eventually disappears perhaps as a result of slow-working modifiable factors; *Lygaeonematus abietinum* Dahlb., which may be counted among the lasting spruce-pests in many woods, as e.g. in some woods in the Geldersche Achterhoek and also in other countries.

According to GRAHAM *Rhyaciana frustana* Comst. is, in America, generally kept in check by its parasites. If no suitable parasites are available, gradations originate which last for years, as happened in the Nebraska National Forest and in Illinois, Indiana and Kentucky. Unfortunately GRAHAM does not state why the parasites are not efficient in the latter states. Have we here, perhaps, to deal with parasites that may not be counted among the modifiable factors so that they can exclusively have a regulating influence in the phase of natural density?

Finally we may yet mention *Cryptorrhynchus gravis* F., which does not form gradations in virgin-forests and always affects 80% of the mango fruits in the villages of Western Java. Unfavourable weather conditions may temporarily lessen the pest, but the beetles soon increase again in number (VOÛTE 1935).

2. Modifiable factors are present causing a crisis again and again, thus reducing the density of population to a low level. As an example *Diprion pini* L. may be quoted which is eventually controlled by an egg-parasite (BESEMER, DE FLUITER 1932, FRANSEN, THALERHORST) the black arch of which the gradation on the Rominter Heide was checked by illness and parasites.

In some cases the resistance has been lowered to such a degree for certain species that the growth in the phase of natural density undergoes no check worth mentioning. This is the case with many pests of our cultivated plants: rice-borer (VAN DER GOOT), mango beetle (VOÛTE), pepper bug (VAN DER VECHT), large cabbage white in our cabbage fields, etc.

Resuming we may say that the impoverishment of the fauna endangers the stability of the community, and gives rise to the occurrence of gradations. The stronger the impoverishment the greater the chance of gradation.

The increase of the instability of the community naturally originates as well when the virgin-forests are poor in species, e.g. as a result of the rough climate. It is true that here the climate controls the occurrence of insect-pests; if, however, insects are able to develop in this climate, they meet with little resistance afterwards. An instance of this is furnished by the insects destroying too old trees, as the catastrophe-theory teaches. As soon as the woods become too old one of the resistant factors is disposed of for this group of insects. The wood, poor in species as it is, contains too few regulating forces to keep the insects in question in check.

The ruinous influence that the importation of *Lygaeonematus erichsoni* Hartig had on *Larix laricius* K. Koch in Labrador points to the same phenomenon. The biocoenosis of the impoverished virgin-forest could offer no resistance to the activity of this insect.

7. OTHER WAYS IN WHICH THE DENSITY OF POPULATION MAY BE REGULATED

Many people are of opinion that the density of population can be exclusively regulated by the climate (BODENHEIMER 1928 and probably also UVAROV 1931). As, however, climatic influences equally affect dense populations and less dense ones, it is impossible to ascribe a regulating activity to them. The regulating activity is, as CHAPMAN observes, a biotic phenomenon. In this connection it may be observed that in some cases appearances seem to point to the regulating activity of the climate. Thus JANISCH (1930) observed that the wholesale increase of *Prodenia littoralis* Boisd. in Egypt, lasts from spring to the end of July. After that *Prodenia* disappears, not as a result of the activity of parasites, but of that of the climate. In such a case the important thing is the climatic influences that destroy the entire population with the exception of a small number that has been able to escape this destruction for some reason or other. If this latter number does not depend of the density, but, e.g., on the size of the shelters, the climate has indeed a regulating influence. If the number does depend on the density, a changing number will stand the unfavourable times, so that in that case, we cannot speak of real regulation.

Indirectly, the climate may influence the regulation. Thus, according to CHAPMAN (1939), researches by COOK, SEAMAN and others, have shown that the occurrence of a plague of *Agrotis* *orthogonia* Morr. is decided by the degree of dampness of the soil during the period in which the larvae are feeding in the year preceding that of the plague. Warm regions with little rain are favourable to this caterpillar. If the soil is damp, the larvae feed overground, which they do not on dry soil, and are within reach of their parasites and predators. So in this case the climate promotes the regulating influence of parasites and predators. The same thing happens with the parasitizing of *Phyllocnistis citrella* Staint by *Ageniaspis* sp. A damp atmosphere gives to the citrus leaf into which Phyllocnistis bores, a thin cuticle, thus making the caterpillar accessible to the parasite. How great this influence of the climate can be is shown by my research relating to this subject (1935).

THOMPSON and ELTON are of opinion (cf. GRAHAM) that regulation of the density is effected by emigration. Through this the animals would reach a less favourable area, where mortality is higher, so that, in the original area, the density keeps on the same level and does not get too high.

Many examples are known where the density of a species is regulated in this way. Thus certain species of locusts become migratory locusts in case of overpopulation, thereby causing the notorious plagues. In this connection I want to refer to researches of UVAROV (1933), FAURE (1932) and others. From my own research after the influence of overpopulation on the migration of *Calandra oryzae* L. it appears that the migration-urge in this beetle is only present over a certain density, and increases in proportion to it. On the level where migration begins to occur, the dependent general factors become active too, causing, e.g., the egg-production to diminish (1937/38). In forestry, too, such a way of regulation occurs. From BESEMER's research it may be concluded that *Diprion pini* L. cannot maintain itself in woods, but can do so in its potential foci, viz., the isolated pine, growing on very poor soil. During a gradation the wasps move in great numbers to the woods where mortality is 100%. As a result of this the density in the potential foci must decrease, or at least be less high than it would have been without emigration.

So, although migration may, indeed, have a regulating influence on the density of population, this manner of regulation may certainly not be regarded as the most important. In *Calandra*, e.g., the density is kept at a comparatively high level, in *Diprion* this will undoubtely be the case as well, although exact data are lacking. Also with migratory locusts migration only occurs after a strong overpopulation or perhaps other unfavourable circumstances. The natural density of our forest-insects is certainly not such that their migration urge is influenced by it. When this is not the case migration will never have a regulating influence. It may, however, contribute to the species increasing more slowly. For, as long as the migration-urge is not influenced by the density an identical percentage of a dense or a less dense population will migrate to an unfavourable region.

Closely connected with the regulation by migration is that occasioned by the occupation of a certain territory by every animal, as is often the case with birds or with colonies, as can be observed with ants. It is clear that by this the density of population can never pass a certain limit.

In the above I tried to give an impression of the way in which, in my opinion, the density of forest-insects is regulated in natural surroundings. Further research will probably induce me to revise my opinion or to complete it. In the present state of science we shall, I think, have to stick to this opinion. Therefore a research after the way how to fight or rather prevent insect-plagues, will have to be based on the above mentioned opinion.

I am convinced that a forest-entomology is possible on the basis set forth in the preceding pages. It will always keep the same ideal in view, but will work along different lines. We shall have to consider seriously if it is not desirable to import the exotics used in our woods as undergrowths, with some of their enemies, and the enemies of those enemies, a thing which, up to now, has always been carefully avoided.

I am convinced that we are, in this respect, on the verge of a new phase in the development of forest-entomology.

8. CONCLUSIONS

1. The division of the resistance factors as given in Acta Biotheoretica (Voûte 1943) is taken as the point of departure.

2. Climate and other a-biotic factors always permit a growth of the population within the area of distribution of a species. That a population does not, eventually, become denser is the result of the activity of biotic factors.

3. When a population becomes denser, the selective independent factors – principally the polyphagous predators and para-

sites will at first have a regulating influence. Many of these polyphagous predators will viz. begin to specialize on the species in question. In the long run this influence is increased by that of the modifiable factors especially the monophagous parasites, which increase as a result of the higher density of their host.

If, notwithstanding these factors the density increases further, the value of the selective independent factors will rapidly decrease, thus increasing the possibility of further growth of the population.

This growth is put to an end by the general dependent factors, which stabilize the density at a high level, or by the modifiable factors mentioned above. In this case a crisis occurs, and the population is reduced to a low level.

4. Up to the moment when the value of the selective, independent factors decreases, the density of the population is that called: "natural density". This density must not be confused with the "eiserne Bestand" of SCHWERDTFEGER and his collaborators, which, if I have rightly understood ENGEL, has as its topmost limit the density where the selective, independent factors begin to show a regulating activity.

The phase in the growth of the population where the activity of the selective, independent factors decreases, is called the "escape-phase".

The phase where the density of population is reduced to the level of natural density is called the "crisis".

5. The climate exercises a considerable influence on the growth of a population.

6. The mixed virgin-forest possesses a great resistance against the occurrence of insect-pests. In such a forest the density of the population is generally the natural density.

7. The transition from virgin-forest to cultivated wood nearly always means a faunistic impoverishment of the wood.

8. The importation of exotics generally means a faunistic impoverishment of the wood in question.

9. Faunistic impoverishment of a wood is accompanied by a decrease of the regulating activity of the selective, independent factors. This means that the insect population will easily reach the escape phase. By this the stability of the community is decreased, and the chances of an occurrence of insect-plagues increase.

10. The checking of the faunistic impoverishment of our

cultivated woods will be the most important problem of a forest-entomology aiming at the laying out of forests with a great resistance against the occurrence of insect-plagues.

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DE L'INFLUENCE DU GANGLION SUS-OESOPHAGIEN SUR LES FONCTIONS DU PIED DE L'ESCARGOT (HELIX POMATIA LINNÉ)[1]

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INTRODUCTION

Avant de faire certaines communications relatives à l'influence du ganglion céphalique sur les fonctions du pied de l'escargot, nous désirons remémorer quelles sont ces fonctions et de quelles parties – au point de vue anatomique – se compose l'objet sur lequel nous expérimentons.

Dans tous les muscles il faut distinguer la tonicité ou le tonus et le mouvement.

1°. Le tonus est une légère tension involontaire qui maintient les muscles striés somatiques dans une certaine position. – Dans les sacs musculeux ou muscles lisses creux, cette tension cause un enveloppement étroit du contenu, produisant un certain turgor. Ce contenu, formant une sorte d'axe liquide, favorise les mouvements antagoniques des différentes portions de ces muscles; il en est tenu compte dans la position des muscles leviers ou squelettiques par rapport avec les membres ou phalanges à mouvoir (antagonisme fixe).

2°. Le mouvement des muscles-leviers se produit sous l'influence de l'innervation rachidienne ou spinale qui cause les mouvements dits: volontaires. Les mouvements des muscles creux ont lieu sous l'influence de l'innervation viscérale, du système nerveux autonome; ils provoquent un changement de position de l'organe ou – si les différentes portions du muscle se contractent et se relâchent en zones transversales – des mouvements péristaltiques. L'objet qui nous intéresse spécialement en ce moment est le pied de l'escargot ou, dans un sens plus restreint: la sole ventrale d'un sac musculeux caractéristique. La figure 1 représente des coupes de ce pied et la paroi de la tunique épidermo-musculaire située au-dessus, à la hauteur de l'anneau oesophagien. Dans la moitié gauche de cette figure se trouvent les détails suivants d'éléments musculaires, tous composés de fibres lisses et couverts par l'épiderme (12), à savoir:

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[1] Exposé pour la Société Néerlandaise de Zoologie à sa séance à Utrecht du 11 décembre 1943.

1. muscles circulaires; 2. muscles transversaux; 3. muscles transversaux diagonaux; 4. présentés plus ou moins en travers: a. muscles longitudinaux, b. muscles longitudinaux diagonaux, c. muscles obliques.

En outre, on a représenté les éléments nerveux suivants: 5. ganglion sus-oesophagien; 6. commissures latérales; 7. ganglion sous-oesophagien, ganglions pédieux inclus; de là partent, plus ou moins accouplés: 8. les nerfs pédieux sensu stricto qui relient le ganglion sous-oesophagien au réseau nerveux du pied.

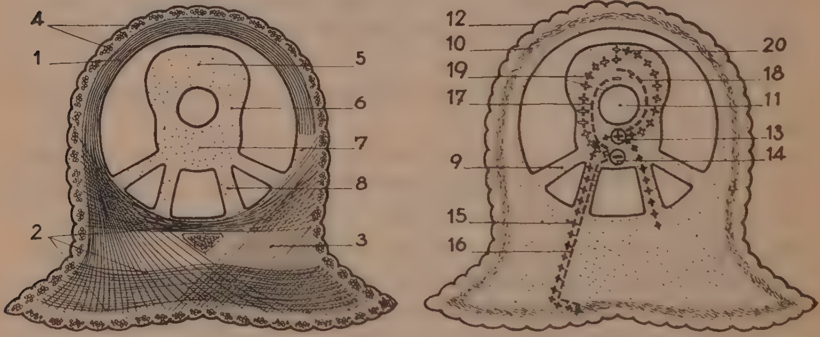

Fig. 1. Explication dans le texte.

La moitié de droite nous montre les détails suivants des éléments nerveux: 9. nerfs pédieux (épipodiaux) qui se ramifient spécialement dans la paroi latérale ou dans le cou. Finalement, les nerfs pédieux sont en relation avec 10. le plexus nerveux, le réseau composé de neurones dans la tunique épidermo-musculaire et dans la sole ventrale du pied et leurs arborescentes anastomosantes; 11. orifice de l'anneau oesophagien.

Le pied de l'escargot présente les phénomènes suivants:

1. des contractions rythmiques, se propageant en ondes le long de la sole et qui jouent un rôle dans la locomotion, l'action de ramper. Nous n'avons pas étudié ce péristaltisme et ne lui accorderons pas d'attention par la suite.

2. contraction et décontraction simples.

3. la tonicité. Le pied de l'*Helix* au repos, une longueur constante étant assurée, conserve une certaine (légère) tension et doit donc être considéré comme le siège d'un tonus statique; la chaleur le fait diminuer.

La périphérie.[1]) Nous mesurons le tonus et la contraction au mécanogramme. A cette fin, le pied est placé dans un appareil distenseur; si dans cet état nous lui faisons porter une charge telle qu'un allongement continu se produise par étirement, l'enregistrement nous donnera un diagramme temps-longueur comprenant une phase de distension et une phase de restauration partielle (le recouvrement ou „recovery") qui suivra la suppression de la charge.

S'il nous était permis de supposer que l'état du muscle ne change pas, le diagramme de la réaction de la périphérie serait analogue à la courbe dite „de BINGHAM" (fig. 2, courbe 2–3a–4a–5a–6) (c.f. POSTMA, 24). JORDAN considérait cette courbe comme une preuve de sa théorie: que le muscle se comporte dans ces circonstances comme un médium visco-élastique avec une limite d'écoulement (le seuil de la force d'allongement), dans lequel médium cette charge, quand elle excède le minimum, est portée durant l'allongement par une résistance visqueuse, tandis que parallèlement, certains éléments du muscle sont étendus par élasticité. Pendant la phase de recouvrement ces éléments produisent un raccourcissement (5a–6) dès la suppression de la charge.

Dans la pratique le cas ne se produit jamais exactement comme nous l'avons décrit: l'état musculeux change; le pied manifeste pendant l'allongement une contre-réaction neuro-musculaire. De même, la résistance est activée, ce qui est démontré d'une manière concluante par l'antagonisme entre cet accroissement du tonus et l'excitation tonolytique. L'influence modératrice de celle-ci produit moins d'effet sur le tonus si l'excitation est appliquée pendant l'étirement que quand on provoque l'inhibition avant la charge se fasse sentir (POSTMA, 22). Non seulement l'allongement agit comme un excitant, mais encore la tension est perçue et même d'une manière spécifique. La tension faible produite par une charge d'étirement plus légère fait augmenter le tonus; la tension forte, causée par une charge plus lourde, fait diminuer le tonus. Ces influences sont démontrées par l'action tardive et sommative de ces charges dans la courbe d'extension précédée par l'intervention d'une contraction tonique survenue après l'élimination de toute résistance extérieure. Il est donc possible de trouver une charge d'étirement neutre ou indifférente qui ne fasse pas augmenter le tonus dans une proportion supérieure à celle déjà produite par l'allongement

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[1]) C'est le pied, privé de tout l'anneau oesophagien, qui ne possède que le réseau nerveux. En ce qui concerne le plexus, il faut remarquer que le réseau nerveux permet au pied de la *Limax* de se contracter et de se distendre suivant des zones transversales qui assurent les ondes de la marche rampante même après l'ablation de l'anneau oesophagien. Le plexus est en état de régler le mouvement; on peut donc le comparer, quant à ses fonctions, au plexus d'AUERBACH. Dans la structure du réseau on peut distinguer une concentration sous la forme d'une échelle. On ne trouve pas cette différenciation dans le pied de l'*Helix*; les ganglions étant extirpés, l'animal n'est plus capable de ramper. La faculté de provoquer un mouvement péristaltique semble localisée ici dans les centres supérieurs, ce qui nous autorise à dire que le plexus de l'*Helix* est moins autonome que celui de la *Limax*.

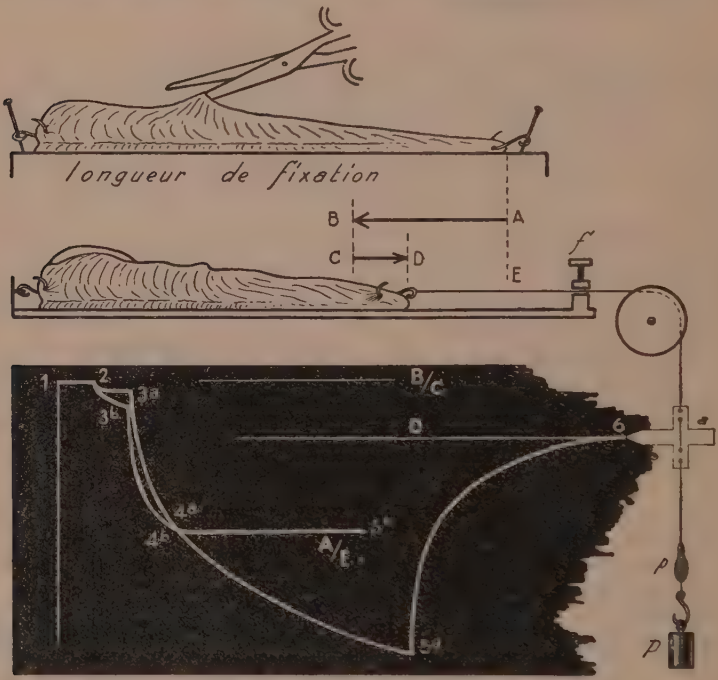

Fig. 2. En haut: pied d'escargot amputé, fixé sur une plaque de cire, (longueur de fixation) et sur lequel on procédera à diverses opérations (la tunique épidermo-musculaire est ouverte du côté dorsal).
Au dessous: pied transféré à l'appareil d'étirement (contraction A–B). A l'extrémité de droite le frein (f) par lequel le pied peut être libéré du poids. Le fil d'étirement passe par le frein, sur une poulie et supporte successivement l'aiguille d'inscripteur (a), le poids de tension (p, 2g) et (facultativement) le poids d'étirement (P).
Sur le papier du kymographe, noirci à la suie: le diagramme de l'allongement et du temps $\left(\frac{dl}{dt}\right)$ (ordonnés: allongement du haut en bas; abscisses: durée. 1 – 2 = 1 min.). Le frein est desserré en 2; en 3 le poids d'étirement est suspendu. Un pied dépourvu des centres nerveux superieurs fait décrire la courbe de tension 2–3a; la courbe d'allongement 3a–4a–5a; le poids est éloigné à 5a; vient ensuite la courbe de recouvrement (recovery 5a–6). Le pied pourvu de ganglions fait décrire la courbe 2–3b tension, 3b–4b–5b l'allongement, avec tonus bastactique dans la partie horizontale.

lui-même, de sorte que cette production de tonus après une contraction tonique ne se manifeste pas dans la courbe d'allongement qui fait suite (Postma, 22).

L'objet à tonus pédieu. 1) Dès l'abord, le muscle du pied pourvu de ganglions pédieux présente à nos yeux une forme différente de celle de l'objet précédent. Le pied est beaucoup plus étalé; les bords de la blessure causée par le détachement de la bourse intestinale manquent d'élasticité; comme ces bords s'appliquent l'un sur l'autre, il n'y a pas de plaie béante. Le taux du tonus (c'est-à-dire: la résistance à l'étirement) du pied pourvu du ganglion sous-oesophagien est donc déjà remarquablement inférieur à celui du pied dont les centres ont été extirpés. Cet état de choses est dû aux ganglions pédieux; aucune excitation spéciale n'est requise; on sait que le grand sympathique des vertébrés possède la même activité autonome.

Quand nous enregistrons la courbe d'allongement (fig. 2, courbe 2–3b–4b–5b) en la comparant à la courbe d'un pied privé de ganglions, nous constatons deux différences:

Concernant le pied avec ganglions: 1°. la partie abrupte du commencement de la courbe est sensiblement plus longue; 2°. après avoir décrit un angle assez brusque (le „coude") la ligne s'aplanit, c'est-à-dire: le pied ne cède plus à la charge d'étirement. Le muscle se trouve dans l'état du tonus portant la charge ou du tonus bastactique.2) Si l'on ne prend pas de précautions spéciales, ces différences ne se manifestent graphiquement que dans le type du diagramme. Le coude peut se produire à bref délai; ces différences concernent alors également la longueur du muscle ou le niveau du tonus. Dans d'autres cas cependant, l'allongement préalable est si considérable que la distension du muscle excède celle d'un pied dont les ganglions sont extirpés, de sorte que les courbes ne se coupent nulle part.

Depuis une dizaine d'années nous connaissons des moyens de comparer quantitativement les réactions du tonus à l'étirement, de même que la régularisation de ces réactions (Postma, 20, 21). Spécialement dans le cas du pied pourvu de ganglions, on procède à l'évaluation de la longueur du muscle ou du niveau du tonus au moment où celui-ci change en tonus bastactique. L'activité tonolytique du ganglion est d'autant plus intense que le muscle est plus allongé à ce moment précis et la tendance à l'augmentation du taux du tonus est d'autant plus faible. Certaines précautions étant prises dans la manipulation du matériel d'expérience, la longueur ou le niveau du tonus peuvent équivaloir la „longueur de fixation" (fig. 2). Lors de la préparation le pied est fixé rigidement sur une plaque de cire, après quoi on procède aux opérations chirurgicales nécessaires. Pendant le transport à l'appareil d'étirement, le pied se contracte plus ou moins fortement (A–B); par la suite on peut lui faire reprendre la longueur de fixation mentionnée (CE = BA) après quoi le tonus bastactique met fin à l'allongement (tableau 1, colonne C)

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1) C'est le pied auquel on n'a enlevé que le ganglion cérébral, de sorte que son tonus est encore sous le contrôle des centres nerveux qui chez beaucoup de limaces sont logés dans des ganglions pédieux séparés, mais qui chez l'*Hélix* sont confondus avec d'autres ganglions pour former le ganglion sous-oesophagien.

2) Dérivé de: *τονος βασταχτικός* = une tension qui porte la charge.

Le niveau mentionné ci-dessus peut nous servir de base de comparaison ou de témoin ce qui nous permettra d'observer l'influence exercée par les modifications des conditions expérimentales. La première courbe de distension nous fait connaître la relation entre la diminution du tonus et la tendance à un accroissement du tonus, par l'étude de l'inclinaison de la courbe d'extensibilité avant que le coude se produise dans la direction du tonus bastactique. Si la ligne est oblique dès le début, c'est que le ganglion met peu d'activité à remplir sa fonction tonolytique tandis que cette activité est grande si l'appareil enregistre au début de l'expérience une descente presque verticale (fig. 2, à partir de 3b).

Deuxièmement nous avons réussi à remettre entièrement à l'état tonique primitif un pied que nous avions allongé; en observant certaines conditions, nous avons suscité une „contraction tonique" qui a eu pour résultat l'enregistrement d'une série de courbes (courbes successives). Après avoir noté la capacité de reproduction de ces courbes, nous pouvons modifier les conditions expérimentales et tirer nos conclusions des variations obtenues.

Un examen plus approfondi a révélé que le pied avec ses ganglions pédieux réagit au poids de la charge d'étirement, c'est-à-dire: de la même manière que la périphérie mais à un degré plus intense. Une charge d'étirement légère provoque une augmentation du tonus: suivant une série de courbes successives le niveau du tonus bastactique s'élève en escalier. Une charge d'étirement lourde cause une réduction du tonus: au début la ligne est presque toujours verticale; le niveau du tonus s'abaisse suivant les courbes successives. Il existe donc une charge indifférente, qui n'affecte pas le tonus (cf. POSTMA, 21a, Abb. 2, p. 1154). Cette charge doit être déterminée pour chaque individu. Cependant la première courbe de distension se trouve au même niveau que la longueur de fixation – indépendamment du poids de la charge d'étirement.

TABLEAU 1

Objets à tonus pédal; longueur de fixation 5¼ cm

	Application de Cl Na au G. sous-oesophagien		Contrôle-objet	Application de cocaïne
	ventral	dorsal		dorsal
Niveaux en cm du tonus bastactique:	*6.05*	**4.45**	5.30	*6.05*
	A	B	C	D

L'étude de cette fonction régulatrice de tonus des ganglions pédieux a révélé que nous avons affaire à deux centres: un centre dorsal (13, fig. 1) qui provoque l'accroissement du tonus et un centre ventral (14) qui en cause la diminution. Il est possible d'activer et de calmer ces centres, aussi bien par des moyens chimiques que par l'action électrotonique du courant continu. La baisse du niveau du tonus bastactique peut donc être causée par la narcose ou l'étourdissement du centre excitateur ou par la stimulation du centre inhibiteur (voir tableau 1, colonnes A et D). Dans le dernier cas, nous constatons un effet secondaire remarquable: la fonction de contraction et la production de tonus par l'étirement ont également diminué. Ce phénomène ne se produit pas quand le tonus est réduit par l'anesthésie du centre dorsal. C'est pourquoi nous désirons marquer la différence entre ce dernier cas d'inhibition du tonus (causé problablement par une diminution de nombre des impulsions excitatrices) et une tonolysie du centre réducteur. [1])

La stimulation du centre ventral dans les ganglions pédieux comme l'excitation des nerfs pédieux, au moyen de faibles chocs d'induction (en tant que liminairs pour la tonolysie) a pour résultat la diminution du tonus. Cet effet est accompagné – si l'on prolonge suffisamment l'expérience – d'une impuissance de plus en plus marquée à effectuer la contraction des muscles. Il est donc évident que la fonction du tonus est une fonction de calage de la contraction. La tonolysie est suscitée par des influx nerveux qui parcourent les nerfs efférents (16, fig. 1) du centre réducteur ce qui constitue un second point d'analogie avec le système nerveux viscéral des vertébrés. Intensifions-nous l'excitation, il s'ensuit une phase dans laquelle les fonctions antagonistes (la tonolysie et l'accroissement du tonus) s'équilibrent, de sorte que le mécanogramme est au repos. L'excitation se fait-elle plus intense encore, il ne reste plus que la contraction.

Les ganglions pédieux n'ont pas d'autre influence sur le mouvement du pied de l'escargot que celle qui s'effectue de par le tonus. En relation avec cette fonction tonique, nous connaissons un état optimal sur lequel l'augmentation du tonus (par l'amortissement du mouvement) aussi bien que la tonolysie (par l'affaiblissement du calage) exercent une influence défavorable.

NOUVELLES EXPÉRIENCES

La préparation neuro-musculaire à tonus central. [2])

Grâce aux recherches de Jordan et de quelques-uns de ses collaborateurs (12 et 8) on a appris que le ganglion cérébroïde a le pouvoir de faire monter le seuil d'excitation produisant la contraction; que la contraction provoquée par une excitation de la même intensité est plus forte après l'ablation du ganglion; donc que le centre nerveux cérébral est inhibif, spécialement en ce qui concerne les fonctions motrices, la locomotion.

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[1]) En rapport avec les fibres musculaires striées, Buchthal a pu démontrer que la distension plus au moins intensive du muscle est due à des champs de force électrique. La contraction est alors le résultat d'un affaiblissement de ces champs. Krijgsman (16) a édifié une théorie sur un champ de force électrique en relation avec la fonction des nerfs. D'après eux, nous aurions affaire, aussi bien dans les muscles que dans les nerfs, avec des membranes (la strie d'Amici resp. la gaine de myéline) dont l'état contrôle le bon fonctionnement de ces organes. Nous voudrions attribuer l'inhibition à un renforcement du champ électrique, donc à une stabilisation des membranes ce qui fait monter le seuil d'excitation. La tonolysie fait penser à une dépolarisation de la membrane par une diminution de l'intensité du champ électrique, suivie d'une impuissance fonctionnelle après une phase de transition dans laquelle la sensibilité est plus grande. Un état optimal est donc franchi. Nous

D'après JORDAN le ganglion n'exerce pas d'influence sur le tonus; en apparence l'objet d'expérience n'a pas changé d'aspect après l'extirpation du ganglion céphalique. Le pied est étalé à plat comme précédemment et les bords de la blessure se rejoignent. Le mesurage de la réaction d'étirement ne révèle aucune différence: le type de la courbe est le même que celui d'une préparation à tonus pédieu; au début, diminution du tonus puis, après le coude, accroissement de celui-ci. Le niveau du tonus

TABLEAU 2

Longueur de fixation $5\frac{1}{4}$ cm

	Charge de distension en proportion poids vif	Objets à tonus pédieu	Objets à tonus central		
		Contrôle	Application de ClNa au G. cérébral	Témoin	Application de Cl-cocaïne au G. cérébral
a	$\frac{1}{8}$	5·05		5·10	
b	$\frac{1}{4}$	5·10		5·00	
c	$\frac{1}{2}$	5·30	**4.55**	5·25	5.75
d	$\frac{1}{1}$	5·30	6.60	6.35	5.75
	A	B	C	D	E

Files horizontales (a, b, c, d) donnent les niveaux du tonus bastactique (cm)

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ne nous occupons pas de savoir si la tonolysie est causée par une insuffisance dans le manchon nerveux ou (et) dans la strie Z du muscle.

[2]) C'est le sujet de l'expérience avec son anneau oesophagien tout entier. Nous ne l'avons pas nommé „préparation tonique cérébrale" parce que le ganglion cérébroïde ne possède pas de centre autonome tonique et ne contribue au contrôle du tonus que par réflexe.

bastactique est en général le même, que le ganglion cérébral soit extirpé ou non (tableau 2, cases Da, Db, Dc et Ba, Bb, Bc).

Cependant nous trouvons une expérience décrite déjà en 1888 par YUNG (30) dans sa Monographie de l'*Helix*; cette expérience attire l'attention sur le fait que le tonus lui-même est aussi inhibé par le ganglion cérébral. YUNG tenta de suspendre l'activité du ganglion par la piqûre d'une aiguille rougie au feu; il contrôla ensuite jusqu'à quel point son expérience avait réussi en faisant des coupes pour constater quelle matière cérébroïde avait été détruite et dans quelle proportion. Il fit ainsi l'observation suivante (p. 86, 87):

> „Dans un cas où toute la portion droite du cerveau avait été brulée, tandis que la gauche était demeurée intacte, nous avons remarqué que l'animal retiré d'abord dans sa coquille et étalé de nouveau avait perdu la coordination des mouvements du pied, nécessaires pour permettre la progression. Les mouvements réflexes étaient conservés sur toute l'étendue du corps, mais le bord droit du pied était recourbé en dedans et demeurait en cet état, l'exagérant à la suite d'excitations mécaniques. Cette expérience, que nous n'avons pas réussi à reproduire, indiquerait donc que la partie droite du cerveau, outre ses fonctions propres (sensibilité spéciale), présiderait à la coordination des mouvements d'ensemble dans la partie correspondante du pied."

Comme YUNG n'avait pu constater de réflexes croisés affectant les tentacules, il admit qu'ils n'existaient généralement pas chez l'*Helix*; à notre avis, le mouvement de manège qu'il décrit, a été causé par l'absence uni-latérale de l'inhibition du tonus. Nous avons effectivement réussi à prouver l'influence cérébroïde sur le tonus; mais il y a cette grande différence que, en contraste avec les ganglions pédieux, le cerveau, pour agir sur le tonus, doît subir une excitation préalable. Jusqu'à présent nous n'avons fait usage que d'excitations chimiques (ClNa). Mais l'activité dépend aussi des autres conditions de l'expérience:

En opposition avec le niveau du tonus bastactique d'un pied „tonique pédal" qui, indépendamment du poids de la charge d'étirement, avait été trouvé à la longueur de fixation, nous avons constaté que le niveau s'abaisse, le ganglion sus-oesophagien étant présent, si l'on fait usage d'une charge d'étirement plus lourde (d'un poids égal à celui du corps ou plus élevé que celui-ci) (voir tableau 2, case Dd, cf. Bd; nous notons ce résultat

TABLEAU 3

A	B	I	II	III	IV	V
4e	Stimulation du centre excitateur					Application ClNa, charge neutre
entre 3e et 4e	Phase de compensation			Charge indifférente		
3e	Stimulation du centre tonolytique			Application Cl-cocaïne charge indifférente	Charge lourde	Application ClNa, charge lourde
2e	Freinage du centre excitateur		Courbes successives, charge légère			
entre 1e et 2e	Phase de compensation				Application Cl-cocaïne charge lourde	
1e	Freinage du centre inhibiteur	Charge de tension (p, Fig. 2)				

Colonne A: phases d'activité du ganglion sus-oesophagien; colonne B: effets déduits des résultats; colonnes I–V: conditions de l'expériance.

au tableau 3, case IV–3). Nous constatons donc l'activité spéciale d'une charge d'étirement lourde qui seule incite le ganglion à réduire le tonus.

L'activité analogue obtenue par une excitation est démontrée clairement par le niveau des courbes successives. Après avoir déterminé un poids „neutre" (fig. 3, courbe „normale", indique le niveau correspondant), on applique du chlorure de sodium au ganglion cérébral avant d'ajouter à la charge après la contraction tonique. Les courbes successives qui se profilent ensuite font constater une tonolysie; le niveau, non dépassé jusqu'ici, au dessus duquel des contractions se produisaient, est actuellement franchi.

Ces résultats sont parfaitement en accord avec ceux que l'on obtient par l'émoussement du ganglion. Sur le tableau 2, la case

Ed démontre clairement par rapport à Dd que dans le cas où un étirement est effectué par un poids plus lourd, l'activité causant la diminution du tonus, produite par cet étirement-même, ne se manifeste pas; le niveau se transcrit plus haut que le niveau de l'expérience sans anesthésique, (noté au tableau 3, case IV, 1/2).

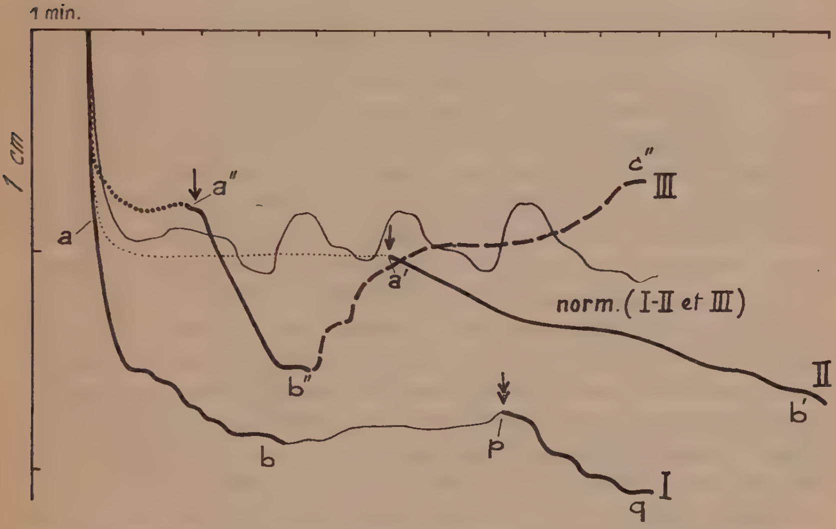

Fig. 3. Courbes successives d'allongement du pied de l'escargot dont le ganglion cérébral est encore présent. En ordonnées: L'allongement (en cm), causé par la charge. En abscisses: la durée en minutes. Expériences concernant l'excitation chimique du ganglion cérébral. Le myogramme „normal" donne le niveau du tonus du pied à ganglion non stimulé. Après la contraction tonique nous avons appliqué du chlorure de sodium au ganglion. Cette stimulation produit une inhibition évidente: comparez le passage du niveau normal: dans la courbe I de a à b immédiatement après le chargement tandis que de p à q la tonolysie se reproduit; dans la courbe II au bout de 5 minutes d'étirement et tonus bastactique en a′; ensuite sans interruption (jusqu'à b′) pendant 8 minutes; dans la courbe III au bout de 1¾ min. de a″ à b″ où une contraction intervient (jusqu'en c″). Nous observons ici une réaction en deux phases opposées, qui fait penser à celles que l'on provoque par une excitation chimique des ganglions pédieux (comparez N. Postma (19), fig. 2, page 1243).

Une activité cérébroïde occasionnant la réduction du tonus s'exprime aussi dans les expériences suivantes, contrairement à la réaction de la préparation tonique pédale: Dans les cas en question, une charge neutre se présentait toujours parallèlement avec une charge légère – causant l'accroissement du tonus – et un poids plus lourd, produisant la réduction de celui-ci; en présence du ganglion cérébral, l'action accélérante d'une charge légère ne se produisit que par exception; ce qu'il faut attribuer à l'influence en sens négatif de ce ganglion. (Noté au tableau 3, case II–2.)

Les expériences pratiquées sur un pied d'escargot qui n'a pas encore été soumis à l'allongement, ont donné des résultats contraires à ceux que nous venons de signaler. On ne peut le constater qu'en observant les changements de niveau de la première courbe de distente.

Deux séries d'observations furent faites dans une succession d'expériences sur des pieds pourvus du ganglion cérébral, à savoir: dans chaque cas, simultanément sur un pied non soumis à une excitation (témoin) et sur un pied auquel on suspendit une charge moyenne, 5 minutes après l'application de ClNa au ganglion. Les chiffres obtenus démontrent que l'excitation qui précède l'étirement favorise l'augmentation du tonus. Celle-ci est appréciable quand la charge est moyenne (tableau 2, cases Cc à comparer avec Dc; noté au tableau 3, case V–4). Fait on usage d'une charge lourde, l'augmentation du tonus qui devrait résulter de l'excitation est annihilée par l'intervention de la tonolysie, suscitée par la haute tension (tableau 2 case Cd à comparer avec Dd; noté au tableau 3 case V–3). – La narcose du ganglion, jointe à l'emploi d'un poids d'étirement moyen, provoque une baisse du niveau (tableau 2, case Ec, noté au tableau 3, case III–3/4 à comparer avec III–2).

En général on peut dire que le G. sus-oesophagien influence le tonus d'une manière secondaire, c'est-à-dire: en tant que centre de réflexes. La réaction tonique d'étirement se modifie dès qu'il est stimulé. Ces phénomènes peuvent être causés par l'étirement en lui-même, – tout spécialement par l'étirement effectué par une charge lourde (donc: impressions proprioceptives) ou encore par une autre excitation (exteroceptive). L'effet obtenu dépend cependant d'autres circonstances expérimentales, par exemple: la diminution du tonus au cours de l'étirement, ou lui succédant à court délai; hausse du niveau au repos. Cette stimulation du tonus a été également observée quand, par le déclanchement du frein du mécanographe le pied a été soumis à l'action du poids de tension (poids minime), phénomène observé de nouveau au cours des expériences que DE JONG vient d'entreprendre (fig. 4) (pas publié); c'est-à-dire qu'alors le muscle se raccourcit, fait qui n'a jamais été constaté en rapport avec le pied à tonus pédieu.

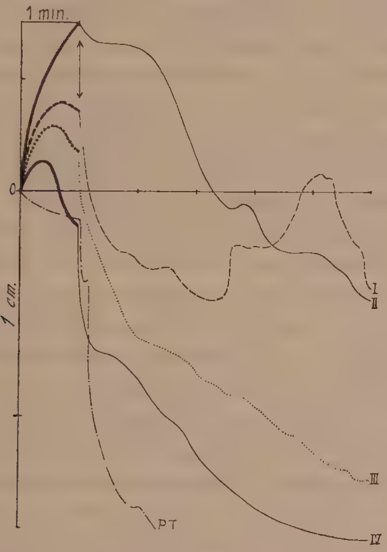

Fig. 4. Myogrammes de quelques pieds d'escargot (de I à IV) avec ganglion cérébroïde intact. En comparaison, la courbe d'un objet à tonus pédieu ou pédal-tonique (P.T.) dont le pied après desserrement du frein (temps 0) cède légèrement sur toute sa longueur sous l'influence du poids de tension, ensuite après une minute (flèche double) le poids d'étirement produit un allongement rapide. Les autres courbes représentent toutes en premier lieu une contraction qui n'est interrompue dans la courbe II que par le chargement; dans les trois autres courbes une descente succède spontanément à un sommet; l'inclinaison en est rendue considérablement plus rapide par le poids réel d'étirement.

DISCUSSION

Si nous désirons interpréter plus en détail les phénomènes toniques centraux que nous avons observés, nous aurons deux problèmes importants à traiter dont l'un concerne la physiologie des nerfs et l'autre, celle du muscle. Le premier se rapporte à l'activité du ganglion: la réduction du tonus peut être causée par l'inhibition du centre excitateur ou par la stimulation du centre tonolytique; l'augmentation du tonus et la contraction peuvent résulter de la stimulation du centre moteur ou de l'amortissement du centre tonolytique.

Franz (10) a déjà fait (en 1919) la description d'une inhibition cérébrale, spécialement en relation avec le réflexe de rétraction des grandes tentacules de l'escargot; ce réflexe est inhibité par des excitations optiques, par la voie de la partie antérieure du cerveau.

Une influence analogue – mais effectuée sur un centre inhibitif et un centre accélérant dans les ganglions viscéraux – a été découverte par van Tiel (en 1940) concernant la régularisation des fonctions du coeur de l'*Helix*. On serait tout d'abord tenté de se représenter le même mécanisme pour le tonus, c'est-à-dire: l'inhibition de deux centres antagonistes dont le centre pédal tonolytique – de même que le centre viscéral inhibitif pour le coeur – possède un seuil d'excitation inférieur à celui des centres excitateurs. Cependant il nous faut remarquer que l'action tonolytique secondaire ne peut être prépondérante dans ce système que lorsque la modération de la tonolysie est affaiblie, c'est-à-dire que quand l'activité du G. cérébroïde diminue. Mais cette action accompagne justement une excitation effectuée après l'étirement (donc après une intensification des réflexes et de l'activité cérébrale) et résulte aussi de l'influence d'une forte tension (charge lourde). Cette activité plus intense cependant aura pour résultat un raccourcissement ou un grade de tonus plus élevé – causé par la réduction de la tonolysie.

C'est pourquoi nous désirons comparer nos résultats à un second antagonisme: la stimulation du centre pédal tonolytique avec son seuil inférieur d'excitation et celle du centre accélérateur. Il y a place ici pour l'effet secondaire auquel nous venons de faire allusion; en même temps on pourra limiter l'étirement par l'intervention de la contractilité à condition que le potentiel de contraction n'ait pas été trop décalé par la tonolysie.

Nous allons nous occuper de chacun de nos résultats séparément et chercher à les expliquer suivant le principe de la double inhibition cérébrale (groupe A) et, parallèlement, suivant le principe de la double stimulation (groupe B). (Voir aussi tableau 3; les chiffres romains qui suivent se rapportent aux colonnes de ce tableau).

I Le frein de l'appareil d'étirement étant déclanché, il se produit un raccourcissement central-tonique caractéristique qui se transforme en une distension. Nous ne constatons cette contraction que lorsque nous faisons usage de la charge de tension (p, fig. 2); la tension obtenue est évidement trop faible pour soulever un poids d'étirement (P). Afin d'expliquer ce raccourcissement, nous pouvons admettre que le pied au repos sur l'appareil ne possède qu'un degré inférieur d'activité.

A. Si nous commençons par la réduction de la tonolysie – intervention qui provoque un raccourcissement – la charge de tension, en suscitant de nouvelles impulsions, stimulera l'activité de telle manière que le freinage du centre excitateur se fera sentir, lui aussi: il s'ensuivra une détente, éventuellement favorisée par une diminution de l'inhibition de la tonolysie, causée par une adaptation du centre.

B. Notons ici une action initiale de la tonolysie qui causera une diminution du tonus ou même une dilatation. L'étirement suscite des stimulus qui feront augmenter le degré d'activité; l'excitation du centre accélérateur aura pour conséquence une augmentation du tonus et une contraction. Ces phénomènes peuvent encore être favorisés par la perception d'une tension faible (poids de tension). L'observation prouva le contraire!

II. Employons-nous une charge d'étirement légère, nous ne trouverons dans les courbes successives aucune différence avec la longueur de fixatation, c'est-à-dire que la fonction pédale qui stimule le tonus est suspendue par le centre cérébral. Si nous avons affaire à une charge „neutre'', nous pouvons admettre que la préparation se trouve à ce moment dans une phase de compensation dans laquelle les influences du centre tonolytique et du centre excitateur sont en équilibre. Le degré d'activité augmente grâce au réflexe d'étirement qui s'ajoute au réflexe de tension. Nous pouvons donc émettre l'hypothèse suivante:

A. Prépondérance de l'inhibition du centre moteur, c'est-à-dire: diminution du tonus de l'objet à tonus pédieu. La progression pédaltonique est annulée.

B. Prépondérance de l'excitation du centre moteur, c'est-à-dire: augmentation du tonus, donc renforcement de la progression pédaltonique. Ce qui est en contradiction avec les faits observés.

III. Le pied étant soumis à l'étirement par une charge moyenne, l'application de cocaïne au ganglion provoque un abaissement du niveau du tonus. Si nous employons une charge indifférente, il se produit dans l'objet de l'expérience pédaltonique un équilibre entre la tendance à l'augmentation du tonus et la tendance à la diminution de celui-ci; la présence du G. cérébral n'y apporte aucune modification. L'état d'activité est donc une phase de transition. Si nous appliquons de la cocaïne, la fonction dont le seuil d'excitation est le plus élevé, c'est-à-dire celle qui influe sur le centre accélérateur, est annulée en premier. Nous pourrions donc supputer les résultats suivants:

A. Prépondérance d'une modération de la tonolysie, donc augmentation du tonus, en opposition avec la diminution constatée.

B. Prépondérance de la tonolysie, qui, en concordance avec le résultat obtenu, sera la cause d'un abaissement du niveau du tonus.

IV. Le traitement du ganglion à la cocaïne durant l'étirement au moyen d'une charge lourde n'abaisse pas le niveau tonolytique. L'étirement au moyen d'une charge lourde produit un abaissement du taux du tonus. Ce phénomène peut avoir pour causes: l'intervention de la tonolysie ou (et) le freinage du centre excitateur. L'étourdissement par la cocaïne a donc pour résultats:

A. La diminution de l'inhibition causant la restauration de la longueur de fixation, ce qui a été constaté.

B. La réduction de la tonolysie ce qui conduit également à la restauration de la longueur de fixation. La perte de la capacité de contraction qui accompagne l'étirement avec poids lourd, démontre que la tonolysie et son émoussement sont en jeu.

Va. Le tonus est augmenté par une excitation chimique quand on fait usage d'un poids d'étirement moyen. L'étirement par un poids neutre ne trouble pas l'équilibre établi entre deux tendances antagonistes (comme sous III): nous avons affaire ici à une phase de compensation. Par une excitation au moyen de ClNa, nous rehaussons l'activité centrale et mettons en évidence l'influence exercée sur le centre excitateur.

A. La prépondérance du freinage fera diminuer le tonus, ce qui est contraire à l'augmentation relativement à la longueur de fixation.

B. La prépondérance de l'accélération fera monter le niveau, ce qui a été constaté.

Vb. L'effet de l'étirement avec poids lourd n'est pas modifié par une excitation chimique. L'étirement avec poids lourd fait diminuer le tonus (cf. sub IV). La stimulation de l'activité par une excitation chimique a pour résultat:

A. L'inhibition du centre accélérateur augmente ce qui continuera à abaisser le niveau du tonus. Le résultat obtenu n'est pas convaincant.

B. La stimulation du centre moteur augmente de sorte que la tonolysie disparait et que la longueur de fixation est restaurée. Il y a donc contradiction, à moins que la tonolysie n'ait annihilé la capacité de restauration – ce que l'on peut admettre sans autres.

VI. Le poids indifférent étant déterminé (courbes successives), l'excitation chimique précédant la rapplication du poids a toujours pour résultat l'inhibition. Par analogie avec II nous cherchons à déterminer une phase de compensation qui mette en équilibre les tendances antagonistes. L'intensification de l'activité, obtenue par l'excitation chimique (et l'étirement) fait supputer (ainsi qu'il a été démontré sous II) les résultats suivants:

A. Prépondérance de l'inhibition motrice avec diminution du tonus; ce qui est admissible, mais nous ne pouvons constater aucune influence tonolytique secondaire.

B. Prépondérance de l'accélération du centre excitateur avec augmentation du tonus ce qui est en contradiction avec le résultat.

L'explication donnée ci-dessus est suffisante dans touts les cas excepté le VIème cas. Nous pouvons faire entrer la tonolysie dans les phénomènes du groupe A, si, étant donnè son degré nécessaire d'activité cérébrale, elle se joint à celui de l'inhibition du centre accélérateur, de sorte que – l'activité du ganglion cérébroïde augmentant progressivement – nous pouvons noter successivement les phases suivantes:

1ère phase: Inhibition du centre pédal tonolytique (fig. 1, 17) qui donne lieu de s'attendre à une augmentation du tonus;

2ème phase: Inhibition du centre pédal excitateur (18) qui aura pour résultat une diminution du tonus;

phase de compensation 1–2: équilibre entre 1 et 2; on ne peut constater aucune modification du tonus;

3ème phase: stimulation du centre tonolytique (19) produisant une diminution plus rapide du tonus, ayant pour effet secondaire l'amortissement de la capacité de contraction.

4ème phase: stimulation du centre moteur (20) qui augmentera la résistance et qui éventuellement donnera lieu à une contraction, pour peu que la capacité n'en ait pas été trop altérée dans la 3ème phase:

phase de transition 3–4: équilibre entre 3 et 4, ce qui a été constaté préalablement dans les expériences d'excitation des nerfs pédieux (POSTMA, 22, fig. 2a).

En résumant, nous pouvons donc dire que les résultats commentés sous I et II ne peuvent être expliqués que si nous admettons une double inhibition cérébrale; sous III, IV, V que si nous reconnaissons une fonction stimulante du ganglion sus-oesophagien; tandis que les suites de l'excitation subie avant que l'ont ait commencé à enregistrer les courbes successives (VI) ne peuvent être expliqués que si l'accélération succède à l'inhibition; il est bien entendu que la stimulation exige une activité plus intense du ganglion cérébral que l'inhibition.

La phase motrice (4e) se manifeste probablement aussi par des contractions qui se produisent spontanément en suite d'un allongement souvant considérable – ou qui sont provoquées par l'excitation du ganglion, ainsi que VAN KOERSVELD l'a expérimenté par l'application de différents sels (pas encore publié). Les influx d'étirement disparaissent quand le raccourcissement se produit ce qui fait rentrer l'innervation dans la phase 3 (et 2); une distente a donc lieu qui provoque de nouvelles impulsions d'étirement; on peut donc s'attendre à des contractions rythmiques. Comme la préparation pédaltonique a les mêmes propriétés antagonistes, il est évident que ces contractions peuvent être provoquées tout simplement par des réflexes pédaux; aussi appartiennent elles aux phénomènes toniques pédaux les plus caractéristiques.

Nous avons transcrit les considérations précédentes dans un schéma (tableau 3) auquel il ne faut attribuer d'autre valeur que celle d'une démonstration pratique, pouvant servir au cours des expériences à contrôler la justesse de cette interprétation des phénomènes.

Au point de vue biologique, la signification des résultats obtenus est la suivante: Quand l'escargot veut étaler le pied et que, dans ce but, par la contraction d'autres muscles, il presse dans la tunique epidermo-musculaire du sang et des intestins, il se présente – en rapport avec l'activité du sujet – deux possibilités:

1°. En premier lieu une résistance progressive (le phase) puis, proportionnellement à la pression croissante, la tonolysie se manifeste (poids lourd d'étirement, 3e phase); il s'ensuit une diminution du tonus constatée généralement dès le début du mouvement; la résistance est vaincue, le pied est étendu.

2°. L'activité étant plus intense, le pied se trouve déjà dans la première phase de compensation (1–2); immédiatement, il cède plus ou moins à la pression. Des influx d'étirement font augmenter l'activité et peuvent provoquer la tonolysie. Dans ce cas on peut s'attendre à ce que le pied s'étende plus graduellement; du moins, au début.

Les impulsions d'étirement provoquées par l'allongement conduisent à la 4ème phase qui suspend l'étirement et qui peut occasionner un raccourcissement. Le fait que VAN TIEL a pu exclure une accélération cérébrale du coeur, pourrait avoir rapport à l'automatisme, ce qui rendrait superflue la provocation centrale des pulsations.

Le problème de la physiologie du muscle se formule dans la question suivante¹):

La contraction tétanique qui provoque le mouvement et le tonus qui maintient le turgor sont-ils deux

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[1]) Pour un aperçu plus récent cf. N. Postma, De la plasticité du pied de l'escargot (*Helix pomatia* Linné) et de ses types de raccourcissemet et de rallongement. Proc. Kon. Akad. Wet. Amst. **XLVIII**, 394–405, 1945.

fonctions musculaires essentiellement indépendantes? S'il en est ainsi, les influences toniques du ganglion sus-oesophagien devraient attaquer directement le tonus, ainsi qu'on l'admet dans le cas des ganglions sous-oesophagien.

Il y a environ quarante ans que JORDAN attribuait le tonus des muscles lisses à un phénomène essentiellement différent de celui du tonus des muscles squelettiques.

Le tonus du muscle strié des vertébrés a été défini: secousses ou contractions brusques de différents ensembles de fibres musculaires, commandé chacun d'eux par une fibre nerveuse („motor-units") à action alternative se résumant en tétanos; un certain raccoursissement (moyen) est obtenu, permettant au tonus de se manifester. L'entrée en jeu d'un nombre progressif d'unités produit une contraction lente; l'inhibition centrale de plus ou moins de neurones motrices (et leurs „units") cause une diminution de tonus, les influx somato-motrices étant en décroissance (BRONDGEEST (3), SHERRINGTON (7), ASMUSSEN (1)). L'assimilation respiratoire est d'autant plus active que le tonus est plus intense. En général, on admettait que le tonus des intestins des vertébrés (muscles lisses) était entretenu de la même manière par des impulsions viscéro-motrices.

D'autres font, dans les muscles lisses, une distinction entre les secousses, contractions passablement rapides exigeant beaucoup d'énergie et un mécanisme spécifique du tonus sans dépense de travail (MÜLLER (18), SCHULZ (25), JORDAN (11,12)). JORDAN se représentait une sorte d'enrayement, travaillant, pour ainsi dire, par frottement, qui assurerait une longueur obtenue par contraction et un certain niveau de tonus. Dans la deuxième décade de notre siècle, JORDAN arrive à une théorie vraiment très avancée, attribuant le tonus uniquement aux propriétés mécaniques de la substance musculaire et déclarant que les phénomènes de la périphérie relatifs au tonus, étaient des phénomènes purement physiques. Après 1930 il abandonne cette théorie pour autant qu'il admet que les propriétés de la substance doivent être assurées par des phénomènes physiologiques; mais la réaction d'étirement appartenait d'après lui uniquement à la physique. La raison la plus caracteristique qu'il allègue est que la chaleur diminue la résistance du tonus à l'étirement tandis que la chaleur, au contraire favorise le tétanos. De plus: les échanges gazeux respiratoires ne sont pas augmentés dans la même mesure que l'activité tonique. Cependant, durant cette même période, certaines propriétés du tonus furent constatées, sur lesquelles la chaleur parut exercer une influence favorable.

En premier lieu, JORDAN constata chez l'*Aplysia* qu'un pied refroidi et par là-même flasque, recouvre son tonus quand on lui fournit de la chaleur; il se produit alors une contraction lente dont la tension est minime. Chez l'*Helix* nous-même avons obtenu une restauration du tonus en suite d'une contraction provoquée dans des conditions spéciales par une excitation électrique, après quoi, la température s'élevant les courbes successives se montrèrent plus compliquées. Le poids étant utilisé de nouveau au sommet de la contraction, les courbes se font plus verticales au fur et à mesure que la température monte bien que ce fait ne se produise qu'au début de l'étirement. Cependant au bout d'un temps plus ou moins long, la résistance à l'étirement s'accentue rapidement; la courbe décrit un „coude" et après un tournant brusque elle s'aplanit d'une manière plus prononcée que par une température plus basse (POSTMA, 19). Cela prouve que la chaleur ne fait diminuer la résistance qu'au début: après le „coude", elle provoque une augmentation C'est pourquoi nous nous demandons si peut-être nous aurions affaire à un phénomène tétanique?

Nous n'avons pas pu empêcher que la contraction tétanique n'influence ces phénomènes; il n'est pas possible que le tonus du pied d'escargot soit uniquement un tétanos car, dans le cas où chez l'*Aplysia* la résistance tonique et la contraction lente sont paralysées par une surabondance de Mg, nous pouvons bien encore provoquer la secousse, mais le maintien du raccourcissement échappe à notre contrôle. Chez le *Helix* aussi nous constatons un dualisme: il n'est possible de provoquer une augmentation du tonus qu'au moyen d'un réflexe, par l'étirement avec un poids léger; la stimulation électrique des nerfs pédieux ne peut produire qu'une secousse ou un raccourcissement tétanique qui a le pouvoir d'augmenter la résistance à l'étirement, mais qui se détend presque immédiatement, l'excitation étant suspendue. La restauration du tonus cependant ne présente pas de décontraction au cours de cette expérience qui – en ce qui concerne la durée – ne dépasse pas les limites biologiques. Il est donc prouvé que le tonus du pied de l'escargot n'est pas purement du tétanos, qu'il est probablement tout autre chose.

Le fait que l'inhibition du tonus (par étirement avec poids lourd, excitation des ganglions ou l'application de courants induits aux nerfs pédieux) et l'accroissement du tonus (par étirement avec poids léger) se prolongent longtemps après la suspension de l'excitation montrant une réaction tardive, nous porte à attribuer au tonus un caractère humoral (Postma, 23). En relation avec ce qui précède, nous pouvons supposer que le tonus est basé sur une contracture telle que nous la connaissons dans d'autres muscles sous l'influence d'acéthylcholine [1]). On sait de cette contracture qu'elle déploie peu de tension, que les échanges gazeux respiratoires n'augmentent pas proportionnellement à la tension obtenue ou au raccourcissement et que le froid peut en favoriser les phénomènes. Une telle contracture du pied d'escargot pourrait être une fonction de calage d'un lot tétanique du tonus si celui-ci avait essentiellement un caractère dualiste, dont nous n'avons pu trouver la preuve dans aucun des muscles que nous avons étudiés. Dans ce cas-là le ganglion cérébroïde pourrait controler sans intermédiaire la contraction tétanique et donc aussi la composante tétanique tandis que la part de contracture subirait l'influence des ganglions pédieux.

Relativement à la théorie ci-dessus, il faut encore remarquer que spécialement en rapport avec le tonus des muscles des Vertébrés, l'explication monistique a perdu de son importance, (Langelaan (17), ten Cate (16), Sommerkamp (26), Wachholder (29), van Dijk (9), Bülbring & Burn (5)). Ils distinguent à côté du tétanos ambulant et partiel (d'éléments de muscles striés avec leur innervation somatique) une contracture de fibrilles musculaires à action lente et tonique, à innervation viscérale [2]).

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[1]) Bacq et Coppée (2) ont trouvé de l'acétylcholine et de la choline-estérase chez quelques Mollusques. Mais après ésérinisation il n'y a pas d'effet cholinergique par excitation, de sorte qu'il doit s'agir d'une autre substance susceptible de provoquer une contracture. La réaction tardive pourrait tout aussi bien représenter un phénomène myogène qu'un phénomène neurogène (p. ex. par émission tardive d'impulsions accélérantes, inhibitrices ou tonolytiques).

[2]) Grâce aux recherches de Buchthal nous pouvons nous réprésenter qu'une contracture peut se produire par la voie d'un affaiblissement graduel des champs électriques myogènes, de sorte qu'elle concernerait le même mécanisme que celui sur lequel repose la secousse. L'affaiblissement peut encore s'obtenir par la libération d'une substance. Les résultats obtenus par Szent-Györgyi sur des fils de myosine tendus des moyens essentiellement mécaniques, font entrevoir la possibilité d'un raccourcissement par l'addition d'une substance sans qu'il soit question d'un champ de force électrique.

Les phénomènes toniques que nous avons étudiés ont en commun avec ceux de la composante de contracture des muscles des Vertébrés: le „pied tonique” au bout de la descente de la contraction brusque, le „genou de Funke” le long de la descente, la durée plus extensive de l'état latent, la réaction prolongée au-delà de l'excitation et finalement la qualification de fonction de calage de la secousse tétanique. Si le tonus du pied d'escargot était de même un phénomène hétérogène, l'opposition essentielle des mécanismes du tonus disparaitrait; les différences feraient naître la question de savoir si c'est la cote tétanique (muscle squelettique) ou le lot de contracture (pied d'escargot) qui a la priorité.

RÉSUMÉ

En opposition aux résultats obtenus précédemment nous avons constaté que le ganglion sus-oesophagien de l'*Helix pomatia* Linné a une influence évidente sur le tonus du muscle pédieu.

La seule présence du ganglion n'a pas d'influence: l'ablation du cerveau ne modifie pas la tonicité.

Le ganglion cérébral agit sur le pied de l'escargot en modifiant la tonicité dans le sens positif ou dans le sens négatif, c'est-à-dire en augmentant ou en diminuant le myotonus. Selon l'état fonctionnel ou d'activité du ganglion nous distinguons quatre phases d'activité. En commençant à observer l'activité à son minimum et en passant par ces phases progressives, nous pouvons noter successivement:

1. Freinage du centre sous-oesophagien inhibiteur;
2. Modération du centre excitateur dans le ganglion pédieu;
3. Stimulation du centre sub-oesophageal tonolytique;
4. Renforcement du centre accélérateur dans le ganglion pédieu,

et deux phases de compensation, états d'équilibre, l'un entre 1 et 2, l'autre entre 3 et 4. Les phases 1 et 4 causent un accroissement du tonus, tandis qu'une baisse du tonus est produite par les phases 2 et 3. L'effet de la dernière est accompagnée par un décalage de la contractilité.

On peut augmenter l'activité du ganglion au moyen d'impressions proprioceptives suscitées par l'allongement lui-même ou par l'intermédiaire d'influx exteroceptifs, causés par l'application de chlorure de sodium au ganglion (excitation permanente). L'activité céphalique peut être supprimée si l'on applique du chlorure de cocaïne au cerveau.

Concernant le tonus musculair nous concluons qu'il est basé sur une contracture qui probablement joue un rôle comme fonction de calage à l'égard d'un lot tétanique de la tonicité. Chez l'*Helix* néanmoins la contracture a la priorité si un tétanos se produit.

ZUSAMMENFASSUNG

Im Gegensatz zu früher erreichten Resultaten, konnten wir nun feststellen, dass das Ganglion cerebrale von *Helix pomatia* L. einen deutlichen Einfluss auf den Muskeltonus des Fusses hat. Das Vorhandensein des Ganglions allein hat keinen Einfluss; Extirpation des Zerebralganglions verändert den Tonus nicht.

Das Zerebralganglion kann den Tonus des Schneckenfusses sowohl in positivem als auch negativem Sinne beeinflussen, d.h. es ist im Stande den Muskeltonus sowohl zu erhöhen als auch zu erniedrigen. Je nach dem Wirkungs- oder Aktivitätsgrad des Ganglions können wir vier Phasen unterscheiden.

1. Hemmung des tonushemmenden Zentrums im Ganglion suboesophageale,
2. Abschwächung des tonusstimulierenden Zentrums im Ganglion pedale,
3. Stimulieren des tonuslösenden Zentrums im Pedalganglion,
4. Verstärkung des tonusstimulierenden Zentrums im Suboesophagealganglion,

und zwei Phasen der Tonuskompensation als Gleichgewichtsphasen; die eine befindet sich zwischen 1 und 2, die andere zwischen 3 und 4. Die Phasen 1 und 4 verursachen eine Tonuserhöhung, während die Phasen 2 und 3 eine Tonuserniedrigung zustande bringen. Der Effekt der letztgenannten Phase geht einher mit einer Entkraftung der Kontraktilität.

Die Aktivität des Ganglion cerebrale kann durch proprioceptive Reize hinsichtlich der Fussverlängerung erhöht werden oder auch durch exteroceptive Reize, indem man NaCl auf das Ganglion bringt (Dauerreizung). Die zerebrale Aktivität kann unterdrückt werden, indem man Cocain (hydrochloratum) auf das Ganglion bringt.

Hinsichtlich des Muskeltonus kommen wir zu dem Schlusse, dass dieser auf einer Kontraktur beruht, welche wahrscheinlich eine unterstützende Funktion hinsichtlich eines tetanischen Teiles des Tonus hat. Bei *Helix* hat die Kontraktur dennoch den Vorzug im Falle ein Tetanus mitspielt.

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THE DISTRIBUTION OF SUBSTANCES IN EGGS OF LIMNAEA STAGNALIS L. CENTRIFUGED IMMEDIATELY BEFORE CLEAVAGE [1]

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INTRODUCTION

In the analysis of development, experiments in which the arrangement of egg substances was changed by means of centrifugal force have played an important part. Under the influence of centrifugal force, the contents of the eggs are stratified, the heavier substances accumulating at the centrifugal pole, whereas the lighter components of the cytoplasm are gathered at the centripetal side of the egg. The development of such eggs is not always the same; often it is seriously disturbed, in other cases however, e.g. mostly in Polychaetes and Mollusks, normal larvae can develop from eggs heavily stratified by centrifugation. This has led to the opinion that the substances displaced by centrifugation, particularly fat and proteid yolk, play no part in the determination of the cells; they were supposed to represent raw materials only, destined to be consumed as food during the development of the embryo.

This conclusion was based on the presumption that the egg substances, which have been displaced by centrifugation, do not return to their normal positions within the egg, but remain in an abnormal place and come to lie, therefore, in "wrong" cleavage cells at further development. It is, however, doubtful whether this presumption holds true in all cases. It has to be determined in every case, therefore, whether a readjustment of the displaced substances during further development takes place.

In a previous paper (Raven & Bretschneider 1942), it has been shown that in *Limnaea stagnalis* the injurious effects of centrifuging the eggs during the uncleaved stage are slight, and do not vary much with the stage of operation. There is no increase in mortality up to the time of first cleavage; on the contrary, in eggs centrifuged in the last hour before cleavage the average mortality was 26%, whereas eggs centrifuged between first and second polar body formation had an average mortality of 39 %.

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[1] This paper was completed towards the end of 1943. Its publication has been delayed by war-conditions. Some questions raised in this paper have been further treated in my paper on p. 353 of this volume, which was finished May 1945.

Furthermore, the observations showed that in eggs centrifuged shortly after oviposition a readjustment of the substances displaced by centrifugation takes place, so that a nearly normal distribution of substances may be restored at the time cleavage begins.

Regarding the distribution of substances in eggs centrifuged shortly before the first cleavage, some observations were made concerning the fatty materials of the egg. They showed that these substances are drawn out along the cleavage furrows, when these are cutting through the egg, and are dispersed, in this manner, over a larger region of the embryo. Moreover, they seemed to prove that a transport of these substances through the cell walls may take place.

These observations made desirable a renewed study of eggs centrifuged immediately before cleavage, in order to obtain a better insight in the processes involved in this transport of egg substances from cell to cell.

MATERIAL AND METHODS

69 Sectioned eggs of *Limnaea stagnalis* have been used for this study. They belonged to 5 egg-masses, and had been centrifuged in their capsules within the last 20 minutes before the beginning of 1st cleavage during 5 minutes at a velocity of 3800 revolutions per minute, giving a centrifugal pressure of 1860 × gravity. At various intervals, samples of these eggs were fixed in Bouin's fluid. Together, there are 15 of these samples; the first was fixed during first cleavage, 15 minutes after centrifugation; the last was preserved 92 hours later, at the trochophore stage. The sections, $7\frac{1}{2}$ μ thick, were stained with iron haematoxylin and eosin, with azan or after Dominici.

In 3 of the egg-masses, a number of eggs was divided at the 2-cell stage into 3 groups: *A* with equal or nearly equal distribution of the egg substances ("fat" and proteid yolk) to either of the blastomeres, the plane of 1st cleavage cutting the layers of the centrifuged egg at right angles; *B* with unequal (oblique) distribution of the substances, the axis of centrifugation making an acute angle with the cleavage plane; and *C* with the "fat" zone in one, the proteid yolk in the other blastomere, the axis of centrifugation being perpendicular to the plane of 1st cleavage. Of 110 eggs, taken at random, only 10 % belonged to group A, 41 % to B and 49 % to C. It seems, therefore, that eggs centrifuged immediately before the beginning of cleavage have a tendency to orient themselves on the machine in such a way that the future cleavage plane is perpendicular to the direction of the centrifugal force; this may be due, perhaps, to the elongation of the egg preceding cleavage. Many of the egg samples used for fixation were taken from these selected groups, especially from C.

The cleavage of the centrifuged eggs was not always regular. In many eggs the formation of cleavage furrows seemed to be retarded in the region of the "fat" zone; in this case, cleavage began at the side of the proteid yolk and led to the formation of a trefoil-shaped egg with undivided "fat" lobe. Some of the sectioned eggs of the samples fixed during the first hours of development showed aberrations of cleavage, too: in one case, an undivided egg contained several large nuclei; in other eggs, pluripolar mitotic spindles were found. Probably, these eggs with abnormal cleavage are soon destroyed; in later samples they are not present.

DESCRIPTION OF THE EGGS

The eggs of sample JJ I, fixed 15 minutes after centrifugation, give a true picture of the stratification of the egg substances brought about by centrifugation. Fig. 1 shows an egg of this sample. Cleavage has just begun, the first furrow is indicated by an indentation at the animal side of the egg, whereas the vegetative side is just beginning to become concave. The axis of stratification is, in this case, almost perpendicular to the plane of first cleavage. Three layers can be distinguished. At one end there is a mass of protoplasm of alveolar structure, consisting of a spongy framework of plasm membranes enclosing rather large vacuoles. Many of these vacuoles contain a large dark stained γ-granule. Then comes a rather narrow layer of small α-granules, staining violet blue with iron haematoxylin; in azan-stained sections they are orange red. These α-granules, which represent, probably, the mitochondria of the egg, are distinctly filiform in this section; they are arranged in irregular streams. This layer is situated about at the junction of the future blastomeres, but is shifted somewhat to the left, to the side of the blastomere with alveolar protoplasm; only at the animal side it reaches into the other blastomere. This consists, for the remaining part, of dense protoplasm filled with densely packed β-granules; a few scattered γ-granules, surrounded by a vacuolar space, are also found in this layer and in the zone of α-granules.

The first signs of a redistribution of the egg substances displaced by centrifugation may be observed in some eggs fixed 35 minutes after centrifugation. They concern only the α-granules, which begin to disperse through the egg protoplasm. At 75 minutes this dispersion of the α-granules has increased considerably; in many eggs the intermediate zone, composed by these granules, is hardly discernible. Finally, 100 minutes after centrifugation, this zone has disappeared altogether; the egg consists of two layers only, one of alveolar protoplasm with vacuoles, the other of dense plasm with β-granules; the boundary between these two regions is rather sharp.

Fig. 2 shows an egg of this sample. It is in the 2-cell stage and belongs to group A, in which the egg substances are distributed rather equally to either of the two blastomeres. In this case, the axis of centrifugation corresponds rather well to the egg axis; the animal side of the egg consists of vacuolar protoplasm, the vegetative side of dense plasm rich in proteid β-granules. The boundary between the layers, although rather sharp, is, however, no straight line. At both sides of the cleavage cavity the layer of β-granules has extended to the animal side and reaches almost to the animal pole. This may be due to the derangement of the layers during cleavage, and reminds of the fat substances drawn out along the cleavage furrows, described in our former paper (cf. RAVEN & BRETSCHNEIDER 1942, p. 272). No intermediate layer of α-granules is present. A distinct accumulation of these granules is, however, found beneath the egg cortex at the animal side of the egg; especially at the animal pole they are heaped up in great quantity, surrounding the upper part of the cleavage cavity. This is in accordance to their localisation in normal eggs of this stage.

During the next hours, the sharp line of demarcation between the two sorts of protoplasm remains. When the egg, with the advance of cleavage, is divided into several blastomeres, some of these cells consist of dense protoplasm with β-granules, whereas other blastomeres contain the alveolar plasm without β-granules. Where these two kinds of cells meet, the cell walls form a sharp boundary between the plasm territories; there is no indication of a passage of β-granules through the cell walls. Only in a few cells, which contain both kinds of protoplasm, the two substances mingle at last; when this has occurred, the contents of these cells show an intermediate condition.

At the late morula stage, a new phenomenon makes its appearance. In the cells with alveolar protoplasm, arising from the centripetal half of the centrifuged egg, a new kind of droplets or granules appears. They agree, in the main, with the β-granules in their staining reactions, but they remain somewhat more pale; with azan, for instance, they are greenish blue, whereas the β-granules are deep indigo blue. Moreover, they are, on an average, distinctly larger than the latter. We will call them β^1-granules.

These granules were observed for the first time in eggs, which had been fixed at the morula stage 20 hours after centrifugation; they are only sparse here. With increasing age of the eggs, their number becomes greater.

The egg of fig. 3 belongs to a sample, which has been fixed $21\frac{1}{2}$ hours after centrifugation at the morula stage. The axis of centrifugation made an angle of about 140° with the egg axis, in this case. The section may be subdivided by an oblique line into two parts: yolk-laden cells take the upper left half of the figure, whereas the lower right half consists of cells, which are poor in granular inclusions. A sharp line of demarcation bounds the two sorts of cells; only at the right there are some cells, which contain both kinds of protoplasm. The yolk-laden cells are filled with densely packed β-granules. The cells of the other half contain alveolar protoplasm, with the exception of the outer parts of the cells, where a narrow zone of dense protoplasm has been formed, as in normal eggs of this stage. In the remaining portions of the cells large, pale granules are seen; they are the β^1-granules. These granules are, however, not restricted to the cells of this half, but a few of them may be seen in the yolk-laden cells between the β-granules as well.

In the next hours, the number of β^1-granules in the originally yolk-free cells increases considerably. At the same time, in the yolk-laden cells the density of the β-granules decreases somewhat. In this way, the differences between the two parts of the egg diminish gradually.

During the second day of development, when the egg is in an advanced cleavage stage, a further change of the granular yolk occurs, indicating important chemical processes going on in the egg. Both the β- and the β^1-granules were acidophil; in the stained sections, they took strongly the eosin. Now, basophil granules appear in the cells, staining black with iron haematoxylin. They are coarser than the β-granules. At first, their number is restricted, but gradually they increase in number. At the same time, the β- and β^1-granules diminish and at last they disappear altogether. Thus, in the gastrula stage the coarse basophil granules are the most prominent of the granular inclusions of the cells.

Presumably, these basophil granules arise by a transformation of the proteid β- and β^1-granules. Therefore, in the cells of the original centrifugal half of the egg, which are still rich in β-granules, their number is much greater than in the cells of the other half, containing only a restricted number of β^1-granules. So, even in the gastrula stage the difference of the two halves is still visible in many eggs.

Fig. 4 shows such a gastrula. The archenteron is sectioned longitudinally. The ectoderm and endoderm are clearly discernible. At both sides of the archenteron, a mesoderm cell is visible, recognizable by its darker protoplasm. The outer parts of the ectoderm cells and the inner parts of the endoderm cells contain many acidophil vacuoles, indicating, probably, a beginning ingestion of albumen from the egg capsule fluid; they are particularly large in the ectoderm opposite the blastopore. The remaining part of the cells contains dark basophil granules; they differ in size, but on an average they are somewhat larger than either the β-or the β^1-granules of preceding stages. In the right and the upper part of the figure, these basophil granules are rather sparse, but in the lower left corner there is a group of cells containing much more of them. This group comprises the mesoderm cell of this side and several ectoderm and endoderm cells. The basophil granules are here, on an average, somewhat smaller than in the remaining part of the section, but their total quantity is much greater. The acidophil vacuoles mentioned above are not clearly visible in these parts, probably, because they are covered by the basophil granules filling the cells to their outer border; it is possible, however, that the formation of the vacuoles is suppressed in these cells.

Many eggs of the gastrula stage give a picture comparable to this. As, on the other hand, in normal eggs of this stage no such differences in density of the basophil granules are found, we may conclude that they represent a last remnant of the stratification brought about by centrifugation. As a matter of fact, in a single case even in an embryo of the early trochophore stage, fixed 74 hours after centrifugation, a slight indication of this difference in granule density has been observed. In most eggs of this sample, however, all trace of the original stratification has disappeared, and so it has in all older embryos.

DISCUSSION

1. When the eggs of *Limnaea* are centrifuged within the last 20 minutes before the beginning of cleavage, the egg contents show a stratification into 3 layers: 1. a centripetal zone of alveolar protoplasm, with γ-granules in the vacuolar spaces; 2. an intermediate layer of α-granules; and 3. a centrifugal mass of dense protoplasm with β-granules. This stratification differs from that obtained by centrifugation of the eggs at an earlier stage. In eggs centrifuged immediately after laying the protoplasm is stratified into four zones: 1. a centripetal cap of oil; 2. a zone of clear protoplasm; 3. a layer of α-granules, and 4. a centrifugal layer of β- and γ-granules (cf. RAVEN & BRETSCHNEIDER, l.c., Pl. III). Whereas the two last-mentioned layers can be recognized likewise in eggs centrifuged shortly before cleavage, the two centripetal layers are represented here by the alveolar protoplasm. The substitution of the four-layered by the three-layered stratification is due to the change of two factors: 1°. The formation of vacuoles from the γ-granules and the accumulation of these vacuoles in the centripetal parts of the centrifuged egg (RAVEN & BRETSCHNEIDER 1942, RAVEN 1945). As a matter of fact, in eggs centrifuged after maturation the boundary between zones 1 and 2 is not sharp, in consequence of the accumulation of vacuoles in zone 1 and the major part of zone 2 (cf. RAVEN & BRETSCHNEIDER, l.c., Pl. IV). When these vacuoles augment up to the end of the uncleaved stage, they will increasingly invade the zone of hyaloplasm and efface, thereby, the diversity of zones 1 and 2. 2°. The increase in viscosity of the egg, occurring shortly before the beginning of cleavage (RAVEN 1945) and leading to a less complete segregation of the egg substances.

2. The animal pole plasm, which appears in the eggs of *Limnaea* about one hour before cleavage (RAVEN 1945), is not found again in the centrifuged eggs. This proves that the viscosity of this plasm is relatively low; during centrifugation its components (e.g. the α-granules) are separated and arranged according to their specific gravity. In this respect, it differs from the pole plasms of *Tubifex*, which are gelatinous in nature and are displaced upon centrifugation in coherent masses (LEHMANN 1938).

3. The α-granules, heaped up in the intermediate zone by centrifugation, do not remain in this position. Already at 35 minutes after the end of centrifugation they begin to disperse

through the egg protoplasm, and 65 minutes later the intermediate zone is no longer visible. At the same time, a local accumulation of these granules at the animal pole of the egg can be observed. This agrees with their distribution in normal eggs of this stage. It seems, therefore, that the forces determining the position of these granules in normal eggs are still active in centrifuged eggs.

With regard to the α-granules, the two processes involved in the readjustment of egg materials, distinguished in our previous paper (RAVEN & BRETSCHNEIDER, l.c., p. 276), can be clearly discerned: 1. the dispersion of the substances accumulated by centrifugation, 2. their localisation in special parts of the embryo. This is the more important, as these granules carry, probably, most of the physiologically active substances of the egg protoplasm: indophenol-blue-oxidase, peroxidase, glycogen and, perhaps, vitamin C (RAVEN & BRETSCHNEIDER 1942, RAVEN 1945). We may presume that these substances play an important part in the determination of the cells. Therefore, it is significant that exactly these granules promptly regain a normal localisation in the egg.

It should be noted in this connection, too, that the α-granules occupy the middle zone of the centrifuged egg. Therefore, even in the eggs of group C, with most unequal distribution of the egg substances at the first cleavage, either of the two blastomeres comprises a part of this zone (cf. fig. 1). This, together with their prompt rearrangement, might explain the high percentage of normally developing embryos even from eggs centrifuged at so late a stage in *Limnaea*. Perhaps, in eggs of other species, with a less favorable position of the physiologically important substances in the stratified egg, the effects of centrifugation are far more injurious.

4. Contrary to the α-granules, the β-granules during the first stages of development are not redispersed through the egg. It is true, when the cleavage furrows are cutting through the egg, they are partly drawn out along these furrows, but in the main the boundary between the plasm territories with and without β-granules remains rather sharp. This unequal distribution of the β-granules does not interfere, however, with normal development up to the gastrula or early trochophore stage. This observation pleads in favour of the opinion that these granules, at least during the first part of development, play no important

part in determination, but constitute a nutritive reserve of proteid materials. For this compound of the egg and this period of development, therefore, the old view of "raw materials", serving as a food reserve only, as it was advocated by CONKLIN (1910) for the egg of *Limnaea*, seems to be right.

5. At the late morula stage, in the cells of the centripetal half of the egg, heretofore devoid of granular proteid yolk substances (with the exception of the γ-granules), a particular kind of granules appears, which cannot be identified with any of the granules hitherto present, but resemble the β-granules in their staining reactions and may be, therefore, proteid in nature. A few of these β^1-granules may be seen in the yolk-laden cells of the other half as well.

As to the origin of these new inclusions, three possibilities present themselves to the mind. Firstly, the β^1-granules might arise by a transformation of the γ-granules, which have been found in early cleavage stages both in the centripetal and the centrifugal halves of the egg. As a matter of fact, at the morula stage the characteristic γ-granules, lying in the centre of a vacuole, are no longer visible. Their fate has not yet been fully elucidated. It seems possible, however, that they are used up in the formation of vacuoles during the early cleavage stages. The observation that the β^1-granules are only sparse at first, but increase in number as development proceeds, speaks against their origin from the γ-granules.

Secondly, the β^1-granules might have their origin in a condensation of albumen, taken up by the egg in dissolved form from the surrounding egg capsule fluid. Such an ingestion of albumen takes place on a large scale in later stages of development, when many cells of the gut turn into large vesicular albumen cells. It is certain, however, that this process has already begun at the morula stage.

Lastly, the appearance of the β^1-granules might be the result of a profound change in the proteid metabolism of the egg, in consequence of which the β-granules are broken down, presumably by an increased enzymatic activity of the cells, and the dissolved products transported from cell to cell through the cell walls. The inverse process, the reconstitution of the original proteids, might give rise, then, to the formation of the β^1-granules in cells hitherto devoid of proteid yolk granules. The observation that the increase in number of the β^1-granules in the originally yolk-free cells goes hand in hand with the decrease of the β-granules in the centrifugal half pleads strongly in favour of this hypothesis.

6. At later cleavage stages the acidophil β- and β^1-granules are replaced by basophil granules. The observation of differences in density of these basophil granules, altogether comparable to those found before, with respect to the acidophil β- and β^1-granules, indicates that the basophil granules arise by a transformation of the proteid β- and β^1-granules. Evidently, the staining reaction of the proteid yolk granules is altered in consequence of chemical processes going on in the egg.

RÉSUMÉ

1. La distribution des substances dans les oeufs de *Limnaea stagnalis*, centrifugés dans les dernières vingt minutes avant le début de la segmentation, était étudiée.
2. La segmentation des oeufs centrifugés montrait quelques anomalies. Spécialement, la zone centripète semble mettre obstacle à la formation des sillons.
3. L'oeuf centrifugé montre une stratification en 3 couches: une zone centripète à protoplasme alveolaire; une couche intermédiaire à granules-α; et une zone centrifuge à protoplasme dense contenant les granules-β. Le plasme polaire animal des oeufs normaux n'est pas visible dans les oeufs centrifugés.
4. Dans les premières 2 heures après la centrifugation, les granules-α, amassés dans la couche intermédiaire, se dispersent dans l'oeuf, enfin ils s'accumulent au pôle animal, comme dans les oeufs normaux.
5. Les granules-β, au contraire, demeurent dans la position qu'ils occupent après la centrifugation. La ligne de démarcation entre la partie centrifuge vitelline et la partie centripète sans vitellus reste assez nette. Cette distribution inégale des granules-β n'empêche pas le développement normal jusqu'au stade gastrula ou trochophore jeune.
6. Au stade morula avancé, dans les cellules de la moitié centripète une nouvelle catégorie de granules parait, qui ressemblent aux granules-β dans leur coloration. La formation de ces granules indique un transport de substances protéiques en forme soluble à travers les parois des cellules.
7. Au stade blastula, la coloration des granules protéiques change de l'acidophilie à la basophilie.

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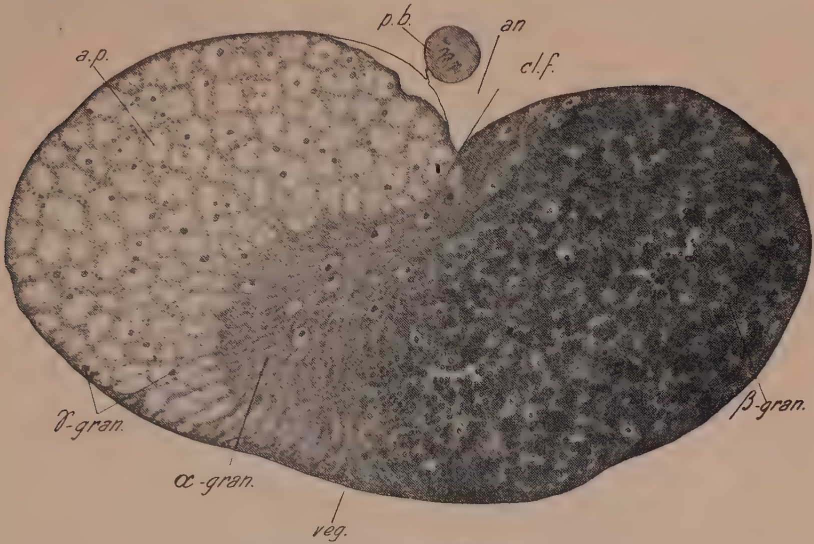


Fig. 1. Egg of *Limnaea stagnalis*, centrifuged shortly before cleavage and fixed 15 minutes later, during first cleavage (JJ I, b). *an* = animal, *veg* = vegetative pole. *cl.f.* = cleavage furrow. *p.b.* = 1st polar body outside vitelline membrane. *a.p.* = alveolar protoplasm at centripetal end. *α-gran.* = layer of α-granules. *β-gran.* = mass of β-granules at centrifugal end. *γ-gran.* = γ-granules in vacuoles.

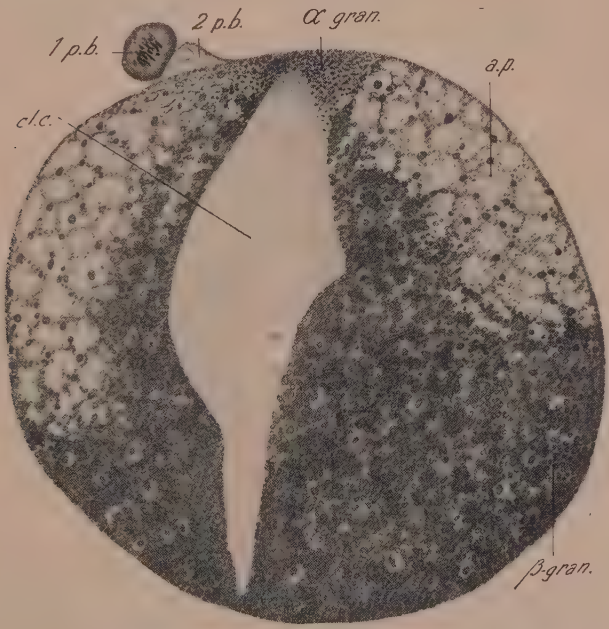


Fig. 2. Egg of *Limnaea*, fixed 100 minutes after centrifugation at the two-cell stage (JJ III, b). *α-gran.* = α-granules accumulated at animal pole. 1.*p.b.* = first, 2.*p.b.* = second polar body. *cl.c.* = cleavage cavity. Other abbreviations cf. fig. 1.

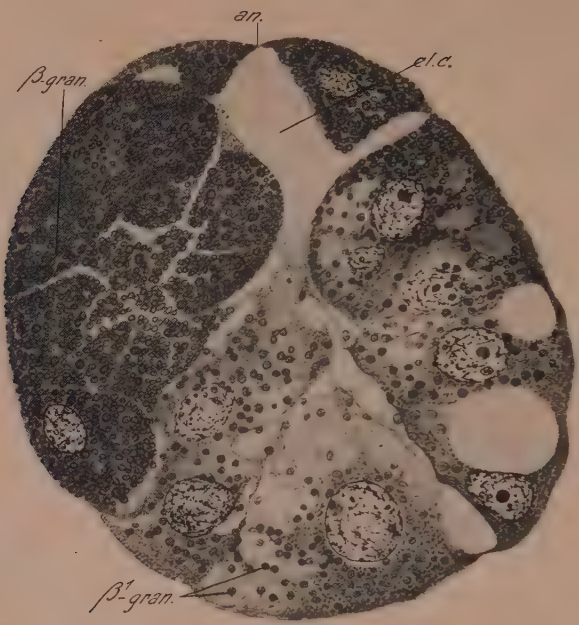


Fig. 3. Egg of *Limnaea*, fixed 21½ hours after centrifugation at the morula stage (JL I, b). β^1-*gran.* — β^1-granules in the centripetal cells with alveolar protoplasm. Other abbreviations cf. fig 1.

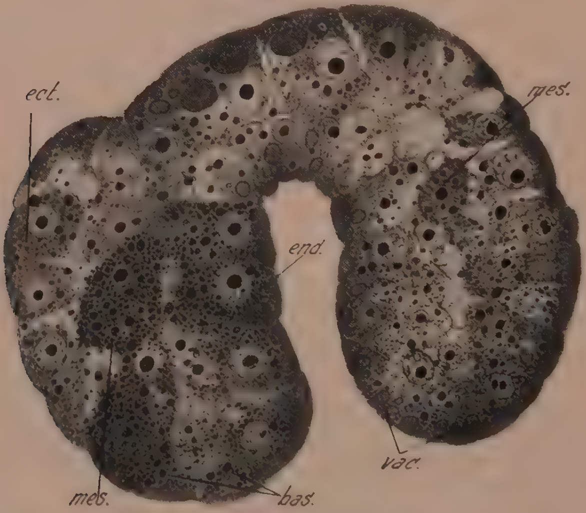
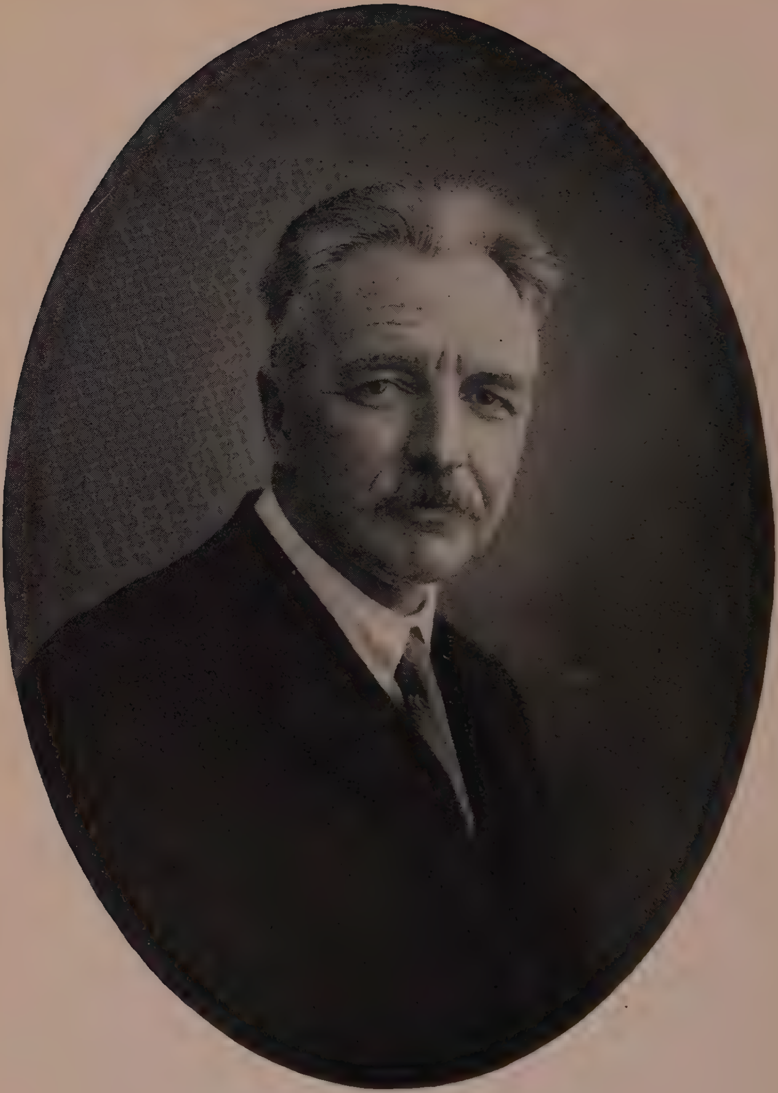


Fig. 4. Egg of *Limnaea*, fixed 50 hours after centrifugation at the gastrula stage (KC II, b). *ect.* = ectoderm. *end.* = endoderm. *mes.* = mesoderm. *vac.* = acidophil vacuoles in ectoderm and endoderm. *bas.* = basophil granules.

DR H. C. REDEKE
ZEVENTIG JAAR

Archives Néerlandaises de Zoologie Tome VII supplément



DR. H. C. REDEKE ZEVENTIG JAAR

Den 29en Augustus had het Bestuur van de Nederlandsche Dierkundige Vereeniging het voorrecht, bij monde van haar Vice-Voorzitter en 1en Secretaris, ons Lid van Verdienste, Dr H. C. Redeke, geluk te wenschen met zijn 70en verjaardag.

Het bereiken van dezen leeftijd in het jaar, waarin wij den heer Redeke dit lidmaatschap van Verdienste van onze Vereeniging mochten aanbieden, was ons een dankbare gelegenheid de vele verdiensten van ons Oud-Bestuurslid (onafgebroken van 1902–1932) en van den Oud-Directeur van ons Zoölogisch Station in den Helder (1902–1929) nog eens naar voren te brengen.

Geboren en getogen Amsterdammer, bezocht hij daar achtereenvolgens de Spieghelschool, het Stedelijk Gymnasium en de Universiteit. Als planten en insecten verzamelend gymnasiast (1886–'92) vond hij een jeugdig-enthousiasten en bekwamen mentor in zijn plant- en dierkunde leeraar, Dr J. C. C. Loman, als student kwam hij onder de leiding van een Faculteit, wier leden thans nog met eerbiedige bewondering genoemd worden: Max Weber, Hugo de Vries, Van 't Hoff, Van der Waals en Molengraaff. In 1896, den 26en Maart, deed hij candidaatsexamen, vatte onder De Vries' leiding de studie der plantengallen aan, deed 8 Maart 1898 doctoraal examen en promoveerde den 24en October 1898, met Max Weber als promotor, op een proefschrift getiteld: Onderzoekingen betreffende het Urogenitaalsysteem der Selachiers en Holocephalen.

Oorspronkelijk was het de bedoeling, dat de jonge doctor als assistent van Professor Weber met de „Siboga" naar Indië zou gaan. Hij was echter reeds gedurende de zomer- en herfstmaanden van de jaren 1896 en 1897 als tijdelijk assistent van den Wetenschappelijken Adviseur in Visscherijzaken, Dr P. P. C. Hoek, aan het Zoölogisch Station in den Helder werkzaam geweest en was daar 1 April 1898 in vasten dienst getreden. Daar bewerkte hij ook zijn proefschrift. Er waren nu groote bezwaren tegen deelneming aan dezen tocht, die hem meer dan een jaar aan dezen nieuwen werkkring zou onttrekken, maar die natuurlijk den jongen bioloog met al haar bekoringen lokte. Er moest een keuze gedaan worden: met de „Siboga" ging de student H. F. Nierstrasz mee, en wij weten thans hoe grooten invloed deze reis op diens levensbaan had, en REDEKE gaf zich geheel aan het werk in den Helder.

Mocht dus een Indische reis, als afsluiting zijner studie, niet voor hem weggelegd zijn, toch kon hij zijn vorming bekronen met een korte reis in het buitenland. Van begin Januari tot eind Maart 1900 was hij werkzaam in het Zoölogisch Station te Napels, waar hij onderzoekingen verrichtte over het maag-darmslijmvlies en den makroskopischen bouw van den tractus intestinalis van haaien en roggen (zie literatuurlijst).

Van toen af lag zijn werk in den Helder, maar niet slechts wetenschappelijke bekoring had deze stad voor hem: den 10den Juli 1901 trad hij er in het huwelijk met de oudste dochter van zijn chef, Mejuffrouw JULIE LAURENCE HOEK, die, zooals wij in de Jaarverslagen lezen, in het Station als adjunct-bibliothecaresse werkzaam was. Als eersten bloesem hunner idylle schonken zij der „scientia amabilis" een „Flora van Helder".

Na het vertrek van Dr HOEK naar Kopenhagen als Secretaris van den Permanenten Internationalen Raad voor het Onderzoek der Zee (Conseil Permanent International pour l'Exploration de la Mer) in 1902, werd Dr REDEKE met ingang van 1 October 1902 belast met de waarneming der betrekking van Wetenschappelijk Adviseur in Visscherijzaken en met de voorloopige leiding van de deelneming van Nederland aan het wetenschappelijk onderzoek der zee. Zijn assistenten waren destijds de tegenwoordige hoogleeraren J. BOEKE en W. E. RINGER, zoomede Dr P. J. VAN BREEMEN, die later gedurende vele jaren visscherij-onderzoekingen heeft verricht op Curaçao. Op 1 Augustus 1903 werd Dr REDEKE belast met de leiding van het inmiddels opgerichte Rijksinstituut voor het Onderzoek der Zee.

Wat betreft zijn relatie tot onze Vereeniging in dien tijd: In 1895 werd de phil. stud. H. C. REDEKE lid der Nederlandsche Dierkundige Vereeniging en den 30en Juni 1895 werd hij door den Voorzitter (HUBRECHT) als nieuw lid welkom geheeten.

Terwijl REDEKE nu Dr HOEK, zooals deze schreef, „wakker assisteerde" in zijn werk voor de Visscherijen, wat we van 1896 af telkens weer in de Jaarverslagen van het Zoölogisch Station kunnen lezen, zoo hielp hij dezen natuurlijk ook als directeur van ons Station. In het jaarverslag van 1898 dankt de heer HOEK den heer REDEKE voor zijn werk aan het Station tijdens zijn afwezigheid. Op 1 Juni 1899 geeft de Voorzitter dan ook aan de Algemeene Vergadering kennis van het feit, dat het Bestuur

Dr H. C. Redeke tijdelijk benoemd heeft tot Assistent-Directeur van het Station.

Der vermelding waard is ook, dat op diezelfde vergadering Professor Sluiter een voorstel aanhangig maakte, om te komen tot een Fauna van Nederland, een voorstel, waarmede toen de heer Redeke onmiddellijk zijn volle instemming betuigde, een instemming, die hij op enthousiaste wijze in daden heeft omgezet, een enthousiasme, waarvan wij nu nog profiteeren door zijn mederedacteurschap in de uitgave van de „Fauna van Nederland", in welke serie hij, zijn belofte in het Jaarverslag van 1900 getrouw, zelf de Visschen heeft bewerkt. Niet alleen de visschen echter interesseerden hem, ook het plankton heeft zijn belangstelling. In het Jaarverslag van 1901 lezen wij, hoe hij het plankton van de Oosterschelde bewerkte en hoe hem de gouden medaille door de Hollandsche Maatschappij der Wetenschappen te Haarlem werd toegekend voor zijn studie over het plankton van het Zwanenwater.

Had Dr Redeke ook aan Dr Hoek hulp verleend bij het assisteeren der leden van de Vereeniging, die op het Zoölogisch Station kwamen werken, waarvoor hem dan ook door den Voorzitter op de Vergadering dank wordt gebracht, als Dr Hoek 1902 naar Kopenhagen gaat (zie boven) benoemt de Vergadering van 21 December den heer Redeke tot Directeur van haar Zoölogisch Station in plaats van den heer Hoek, die tot Eerevoorzitter wordt gekozen. Terzelfder tijd wordt Dr Redeke dan bestuurslid, wat hij blijven zou tot 1932 toe.

Jaarlijks nu brengt de heer Redeke zijn verslag uit over het Zoölogisch Station, welke verslagen in het Tijdschrift onzer Vereeniging te vinden zijn en waaruit zijn vele en veelzijdige werkzaamheden voor het Station onzer Vereeniging blijken. Zij, die tijdens zijn directoraat het voorrecht hadden in den Helder te werken, weten met hoe groote welwillendheid en voorkomendheid gezorgd werd voor de laboranten, een zorg, die wij te meer op prijs moeten stellen, wanneer wij bedenken, hoe dit directoraat van het Zoölogisch Station voor Dr Redeke, evenals voor zijn voorganger (die dit in het Jaarverslag van 1900 nog eens nadrukkelijk stipuleert), slechts bijzaak was naast een drukken werkkring in het belang der Visscherijen. Want vóór alles was Redeke natuurlijk de visscherij-expert, die door zijn vele adviezen de regeering diende en door zijn velerlei wetenschappelijke onderzoekingen de uitkomsten der visscherijen trachtte te verbeteren. Wij kunnen in plaats van een droge opsomming te geven, de lezers verwijzen naar de lijst van publicaties. Speciaal genoemd zij echter het onderzoek met de „Wodan" voor het Internationale Onderzoek der Zee. Moge de tegenwoordige toestand, waarin onze Directeur geheel tot onze eigen beschikking is, idealer zijn, wij moeten, na de oprichters en Dr HOEK, den heer REDEKE dankbaar zijn voor de opoffering en moeite, waarmede hij den grondslag voor den huidigen toestand heeft gelegd, voor de groote zorg, waarmede door hem onze waardevolle bibliotheek werd opgebouwd, voor den goeden naam in het buitenland, die zijn connecties met buitenlandsche geleerden ons Station verschaften. Tijdens het Zoölogencongres in 1901 te Berlijn maakte hij in intiemen kring kennis met mannen, wier namen voor ons reeds klassiek zijn: KARL MÖBIUS, VICTOR CARUS, OSCAR BÜTSCHLI, TH. W. ENGELMANN, en sloot hij vriendschap voor het leven met HANS DRIESCH, KURT HERBST, HANS PRZIBRAM, AUGUST GRUBER, VALENTIN HAECKER, WILLIAM BATESON, EUG. WARMING en A. C. JOHANSEN, den Deenschen hydrobioloog. Tot zijn meer intieme vrienden behooren de hydrobiologen K. A. ANDERSSON, R. LAUTERBORN en E. EHRENBAUM. Ook D'ARCY WENTWORTH THOMPSON en G. ALM behooren tot zijn vriendenkring.

Toen in 1922 de I.V.L. (Internationale Vereinigung für theoretische und angewandte Limnologie) werd opgericht, was REDEKE als vanzelfsprekend bij de oprichtingsvergadering verzocht, die van 3–6 Augustus in Kiel en Plön werd gehouden en tot Februari 1943 vertegenwoordigde hij Nederland bij deze vereeniging. Vanaf de oprichting in 1908 ook was hij mede-redacteur van de „Internationale Revue der gesammten Hydrobiologie und Hydrographie".

Nog een andere zijde van ons veelzijdig Lid van Verdienste mogen wij hier belichten; de Heer REDEKE was ook vol sociale belangstelling. Waar de laatste jaren, tot de oorlog dit verder verhinderde, het Aquarium van ons Station ook voor het Heldersche publiek een attractie vormde, is het de moeite van het vermelden waard, dat reeds het Jaarverslag van 1912 melding maakt van bezoek van Heldersche onderwijzers, arbeiders en onderofficieren. Ook mogen wij hier verklappen met hoeveel succes de jeugd van den Helder de door REDEKE geschreven operettes onder zijn regie opvoerde.

Woonde tot 1915 de Directeur in het Station, na dien kwam dit geheel en al als wetenschappelijk Instituut ter beschikking. In 1916 werd het Rijksinstituut voor het Onderzoek der Zee gesplitst in een Rijksinstituut voor Biologisch en een voor Hydrographisch (thans voor Chemisch, Microbiologisch en Hydrographisch) Visscherijonderzoek. Dr REDEKE, die tot zoo lang, sedert 1912, den titel Adjunct Adviseur in Visscherijzaken droeg (dus ook na den dood van Dr HOEK in 1914), werd benoemd tot Directeur van het eerstgenoemde Instituut en zijn hydrographische assistent, Ir. F. LIEBERT, tot Directeur van het laatstgenoemde.

In 1917 kreeg REDEKE de opdracht een drijvend Laboratorium voor Visscherijonderzoek in te richten. Met dit vaartuig, de „Meerval", dat aanvankelijk te Haarlem, later te Den Helder gestationneerd was, werden tot 1933, in nagenoeg alle provincies van ons land, Zeeland en Groningen uitgezonderd, onderzoekingen op het gebied der rivier- en binnenvisscherij verricht. Het origineele en belangrijke van dit onderzoek blijkt wel uit het feit, dat, toen de heer L. KREITMANN, Conservateur des Eaux et Forêts, de opdracht kreeg voor Frankrijk hetzelfde onderzoek te organiseeren, hij onze „Meerval" vrijwel geheel copieerde.

Voor onze Vereeniging organiseerde de heer REDEKE in den zomer van 1917 te Heumen een Hydrobiologischen Cursus, die een groot succes werd en in 1918 gevolgd werd door eenzelfden cursus in Langweer.

Inmiddels was Dr REDEKE in 1916 privaat-docent geworden aan de Universiteit van Amsterdam, waar hij zijn eerste openbare les gaf op den 10den October 1916 met den titel: „Plankton en Visscherij", en waar hij in den vervolge de Amsterdamsche biologen onderrichtte in de hydrobiologie en planktonkunde en een eigen school van Nederlandsche hydrobiologen stichtte. Zij, die zijn colleges mochten volgen, bewaren de dankbare herinnering aan een heldere boeiende en enthousiaste voordracht, aan tal van interessante demonstraties en aan kennismaking met onderwerpen, waarmede men anders weinig in aanraking kwam. In dit laatste verband herinnert schrijver zich o.a. een college op verzoek over Bibliographie, waarvan het dictaat hem tot op heden practische diensten bewijst. Een bezoek aan de „Meerval" met demonstraties aan boord en kennismaking met het practisch biologisch onderzoek, besloot altijd op aangename wijze den jaarlijkschen cursus.

In 1919 richtte Dr REDEKE met Dr A. B. DROOGLEEVER

FORTUYN en eenige andere biologen het „Vakblad voor Biologen" op. In 1921 was hij de medeoprichter van de „Hydrobiologische Club Amsterdam", een vereeniging van biologen en chemici, waar Dr REDEKE nog immer het contact bewaart met de Nederlandsche jongere hydrobiologen, waarvan zich velen zijn leerlingen mogen noemen. In onze Vergadering van 27 Maart 1920 werd hem opgedragen, in verband met het 50-jarig bestaan onzer Vereeniging, de uitgave voor te bereiden van de Zuiderzee-Monographie, als grondslag voor het onderzoek der Zuiderzee tijdens haar drooglegging. In 1922 zag deze het licht, evenals in 1936 het Supplement hiervan, beide in de keurige verzorging de hand van den redacteur verradende. Ook voor de samenvatting van het eindresultaat van de eerste 10 jaren van onderzoek in het afgesloten IJsselmeer werd hem de redactie opgedragen.

Ook nam Dr REDEKE, aanvankelijk als expert, sinds 1916 als Gedelegeerde voor Nederland, geregeld deel aan de bijeenkomsten van den Internationalen Raad voor het Onderzoek der Zee en van verschillende door dien Raad ingestelde subcommissies en was hij gedurende eenige jaren voorzitter (chairman) der speciale Limnologische Commissie.

Na den dood van Dr HOEK in 1914, dien hij van 1898 af vergezeld had op zijn reizen ten behoeve van de zalmloslatingen in Duitschland, werd hij benoemd tot „Gevolmachtigde voor Nederland volgens artikel X van het Zalmtractaat". In die functie leidde hij de genoemde zalmloslatingen en bezocht in gezelschap van den Ingenieur van den Waterstaat, den heer F. L. SCHLINGEMANN, verschillende stuwen en vischtrappen in België, Duitschland en Zwitserland. Hij was ook gedurende vele jaren met de heeren F. J. M. A. REEKERS en Prof. H. F. NIERSTRASZ, lid van de „Commissie belast met de leiding van en het toezicht op de proefneming met het kweeken en loslaten van jonge zalmpjes in Nederland", welke Commissie op 30 December 1932 werd ontbonden.

In 1929 werd de zetel van het Rijksinstituut voor Biologisch Visscherijonderzoek van den Helder overgeplaatst naar Gouda, waar ook de „Meerval" een ligplaats in den Bleekersingel aan de Varkensmarkt kreeg. Deze overplaatsing noodzaakte Dr REDEKE te bedanken als Directeur van het Zoölogisch Station. Met ingang van 1 Januari 1933 werd hem „onder dankbetuiging voor de in zijn betrekking aan den Lande bewezen diensten, wegens verandering in de inrichting van den dienst, waardoor zijn werkzaamheden overbodig zijn geworden", door H.M. eervol ontslag verleend en werd hij op wachtgeld gesteld, totdat hij in 1938, bij het bereiken van den leeftijd van 65 jaren, gepensionneerd werd.

In den zomer van 1934 vestigde hij zich te Utrecht en hier kwam een andere zijde van Dr REDEKE tot haar recht, een zijde, waarvan onze Bibliotheek reeds in zoo hooge mate had geprofiteerd, namelijk zijn liefde voor het boek. De keurige catalogi van de Bibliotheek onzer Vereeniging getuigen reeds hiervan, thans kon hij deze bibliophiele gave ter beschikking stellen van de Utrechtsche Universiteits Bibliotheek, waar hij van 1 Maart 1940 tot 1 October 1942 als wetenschappelijk assistent behulpzaam was, bij het catalogiseeren en reorganiseeren van den natuurwetenschappelijken en medischen Catalogus. Ook profiteerde men daar van zijn groote bibliographische kennis en zijn liefde voor het oude boek, door zijn hulp in te roepen bij het inrichten van een tentoonstelling van aldaar aanwezige fraaie en zeldzame natuurhistorische plaatwerken (24 Sept.–31 Oct. 1940), die een buitengewoon succes werd.

Het is U geen geheim, dat de heer REDEKE thans bezig is een samenvatting te geven van zijn levenswerk in een boekwerk over de Hydrobiologie van Nederland.

In onze vergadering van 23 Januari 1943 werd besloten den toen spoedig 70-jarige, als een blijk van onze dankbaarheid en waardeering voor het vele werk door hem voor de wetenschap in het algemeen en voor onze Vereeniging in het bijzonder verricht, te benoemen tot Lid van Verdienste. De behoefte ons Lid van Verdienste te eeren en voor het nageslacht iets vast te leggen van de motieven voor onze bewondering en dankbaarheid, deden ons dit korte en natuurlijk onvolledige overzicht samenstellen.

H. ENGEL

DR H. C. REDEKE
ZUM SIEBZIGSTEN GEBURTSTAG
29 AUGUST 1943

Die limnologische Wissenschaft spannt über weite Gebiete. In erster Linie sind natürlich die Seeen, Flüsse und Tümpeln Gegenstand ihrer Forschungen. Sie hat aber auch grosse Grenzgebiete, wo sie in anderen Wissenschaftszweigen hinübergreift aber doch selbständig arbeitet. Ein solches Grenzgebiet ist das Brackwasser mit allem was dazu gehört. Und einer der hervorragendsten Kenner dieses Brackwassergebietes ist der Jubilar, Dr H. C. REDEKE.

Er hat die verschiedenen überaus interessanten Verhältnisse der Brackwasserfauna studiert und darüber schöne Arbeiten geschrieben und er hat uns durch diese Studien einen erweiterten Blick sowohl über die meeres- als die süsswasserbiologischen Verhältnisse gegeben. Vom Anfang mehr auf die marinen Gebiete gerichtet, ist REDEKE – gleichzeitig mit der Aussüssung der Zuidersee, könnte man vielleicht sagen – allmählich zu den Süsswassergebieten übergegangen.

Früher einer der eifrigsten Mitarbeiter der Internationalen Meeresforschung hat er in den späteren Jahrzehnten der Süsswasserforschung seine Kräfte gewidmet und ist er ein wahrer Limnologe geworden. Dies kommt auch darin zum Ausdruck, dass REDEKE bei der Gründung der Internationalen Vereinigung für Limnologie in Kiel im Jahre 1922 anwesend war und später an mehreren Limnologenkongressen teilgenommen hat. Er war ja auch der Leiter des schönen Kongresses in Holland im Jahre 1932. Dabei hatte er Gelegenheit seine grossen Organisationstalente zu zeigen, welche er auch durch Organisation der Brackwasseruntersuchungen und die Einrichtung guter Laboratorien bewiesen hat.

Durch seine vielen Arbeiten in den verschiedenen Gebieten der Limnologie, wobei auch die Fischerei, insbesondere der Lachs nicht zu vergessen sei, hat sich REDEKE als einer der grossen Limnologen unserer Zeit bewährt und die Limnologenkollegen begrüssen daher herzlich den 70-jährigen Forscher, der immer seine Kräfte der uns lieben limnologischen Wissenschaft widmet.

GUNNAR ALM,
Präsident der Internat. Ver. für
theor. und angew. Limnologie.

Stockholm, September 1943.

PUBLICATIES VAN DR H. C. REDEKE

1896

1. De Newfoundlandsche visscherij. – Meded. Visscherij, **III**, p. 100–103.

1897

2. Nieuwste waarnemingen betreffende de voortplanting en ontwikkeling van de Aal. – Meded. Visscherij, **IV**, p. 6–10.
3. Het Biologische Station te Plön. – Ibid., p. 66–71.

1898

4. Onderzoekingen betreffende het Urogenitaalsysteem der Selachiers en Holocephalen. Acad. proefschr. Amsterdam. – Helder, 85 p., 2 pl.
5. Over het darmkanaal bij *Laemargus borealis*. – Tijdschr. Ned. Dierk. Ver., (2), **V**, Verslagen, p. CXVI–CXVII.
6. Een bezoek aan Bergen in Noorwegen en de Internationale Visscherij-tentoonstelling aldaar. – Meded. Visscherij, **V**, p. 108–111, 118–124.
7. De kringloop der gassen in het water. – Ibid., p. 187–189.

1899

8. Kleine Beiträge zur Anatomie der Plagiostomen. – Tijdschr. Ned. Dierk. Ver., (2), **VI**, p. 119–136, 2 pl.
9. Vergiftige Visschen. – Meded. Visscherij, **VI**, p. 13–16.
10. Nieuwe boeken. – Ibid., p. 78–88.
11. Volksnamen van Visschen. – Ibid., p. 109–111.
12. JOSEF SUSTA en de Karperteelt. – Ibid., p. 125–128.

1900

13. Aanteekeningen over den bouw van het maagdarmslijmvlies der Selachiers. – Tijdschr. Ned. Dierk. Ver., (2), **VI**, p. 284–303, 1 pl.
14. Het voorkomen van *Cucumaria frondosa* aan de Nederlandsche kust. – Ibid., Verslagen, p. LIII.
15. Over variaties in de plaatsing der rugvinnen bij *Gobius minutus*. – Ibid., Verslagen, p. LXI.
16. De achteruitgang der zalmvangst in Schotland. – Meded. Visscherij, **VII**, p. 49–55.
17. Garnalenvisscherij aan de Duitsche kust. – Ibid., p. 68–71.
18. Gevaarlijke visschen. – Ibid., p. 106–111, 118–123.
19. Sprot in de haven van Nieuwediep en de Heincke'sche methode. – Ibid., p. 177–190.
20. De Deensche ongevallenwet voor visschers. – Ibid., p. 200–204.
21. Die sogenannte Bursa Entiana der Selachier. – Anat. Anz., **XVII**, p. 146–159.

1901

22. (Met JULIE HOEK), Flora van Helder. – Helder, 216 p.
23. Een en ander over de Prik. – Meded. Visscherij, **VIII**, p. 12–16.
24. Over watervervuiling door fabrieksafval. – Ibid., p. 54–58.
25. Over instellingen ten bate van zeevisschers in Duitschland. – Ibid., p. 69–73, 86–91, 106–110, 121–126, 140–144, 152–155.

1902

26. Note sur la composition du plankton de l'Escaut oriental. – Tijdschr. Ned. Dierk. Ver., (2), **VII**, p. 244–253.
27. Eenige mededeelingen omtrent de samenstelling van het plankton der Oosterschelde. – Ibid., Verslagen, p. XLIII–XLIV.
28. Het voedsel der Zeeuwsche Oesters. In: HOEK, P. P. C., Rapport over de oorzaken van den achteruitgang en hoedanigheid van de Zeeuwsche oester. Bijlage B, p. 103–114. – 's-Gravenhage.
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32. Natuurk. onderzoek van binnenwateren en visscherij. – Ibid., p. 97–110.
33. Drijvende vischeieren. – Ibid., p. 122–125.
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35. Een boek over de visscherij in de Oostzee. – Ibid., p. 139–142.
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1903

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1904

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1905

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1906

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63. Overzicht der uitkomsten van visscherijwaarnemingen met het S.S. Wodan. I. Analyse der vangsten met de ottertrawl in de jaren 1902–1903. – Ibid., p. 28–75.
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1907

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81. Nog eens de Zuiderzeevisscherij in 1906. – Ibid., p. 61–64.
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1908

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89. Over de grens van het Nederlandsche fauna-gebied aan de zeezijde. – Ibid., Verslagen, p. XLII.
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92. De uitkomsten der Zuiderzeevisscherij in 1907. – Meded. Visscherij, **XV**, p. 26–30.
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1909

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101. Eenige aanteekeningen over de bepaling van het zoutgehalte in zeewater van de zuidelijke Noordzee. – Ibid., p. 39–50.
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1910

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109. Temperatuur en zoutgehalte van het zeewater bij drie Nederlandsche lichtschepen en in het Marsdiep 1909. – Ibid., p. 41.
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113. Iets over de kunstmatige teelt van zeevisschen (naar het Duitsch). – Ibid., p. 136–139.
114. Een Nederlandsch Visscherijmuseum. – Ibid., p. 162–170.
115. Over den Snotdolf. – Ibid., p. 188–191.
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1911

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119. Analyse der vangsten met de ottertrawl in het jaar 1910. – Ibid., p. 13–28.
120. Temperatuur en zoutgehalte van het zeewater bij drie Nederlandsche lichtschepen en in het Marsdiep 1910. – Ibid., p. 31.
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128. Wat ontsnapt er door de mazen van den kuil? – Ibid., p. 197–204.
129. Nog eens over den groei der Mosselen. – Ibid., p. 224–228.
130. Over de Wulk en haar beteekenis voor de visscherij. – Ibid., p. 253–260.
131. Garnelenfang in Holland. – Mitteil. D. Seefischerei-Vereins, No. 12, 13 p.

1912

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134. Analyse der vangsten met den ottertrawl in het jaar 1911. – Ibid., p. 17–21.
135. Temperatuur en zoutgehalte van het zeewater bij drie Nederlandsche lichtschepen en in het Marsdiep 1911. – Ibid., p. 25.
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140. Een vernuftig middel om paling te vangen. – Ibid., p. 154–157.
141. Op de grens. – Ibid., p. 183–186, 201–207.
142. Ueber den gegenwärtigen Stand unserer Kenntnis von den Rassen der wichtigsten Nutzfische. – Rapp. Proc. Verb. Cons. Internat. Expl. de la Mer, **XIV**, 6, 35 p.
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1913

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147. Mededeeling over een exemplaar van *Cottus bubalis* Euphr. bij den Helder gevangen. – Ibid., Verslagen, p. CVI.
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149. De Zuiderzee-visscherij in 1912. – Meded. Visscherij, **XX**, p. 13–16.
150. Op de grens (slot van het bovengenoemde artikel). – Ibid., p. 30–37.
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154. Over den tegenwoordigen stand van het Schollenvraagstuk in de Noordzee. – Ibid., p. 169–174.
155. Over de Najaarsharing der Zuiderzee. – Ibid., p. 205–217.
156. Panharing-bakkerij in het groot. – Ibid., p. 241–244.

1914

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158. Idem. Tweede stuk: Over den groei der Zuiderzee-ansjovis. – Ibid., **I**, 2, p. 241–266, 4 pl., 4°.
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161. De uitkomsten der Zuiderzeevisscherij in 1913. – Ibid., p. 21–28.
162. De intocht der Ansjovis. – Ibid., p. 34–38.
163. De Spiering en de spieringvisscherij. – Ibid., p. 51–54, 70–74, 83–85.
164. Een rapport over den Schelvisch. – Ibid., p. 91–99.
165. Een Rijkswandelleeraar voor het visscherijonderwijs. – Ibid., p. 122–124.
166. De Noorsche Kreeft. – Ibid., p. 135–137.
167. Proeve eener biologische statistiek der ansjovis-visscherij in de jaren 1905–1914. – Ibid., p. 141–149.
168. De goede en slechte eigenschappen van sommige zoetwatervisschen. – Ibid., p. 152–155.

1915

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171. Over het Wier en de wiervisscherij. – Ibid.. p. 77–81.
172. Over de Snoekvisscherij in Zuid-Afrika. – Ibid., p. 100–103.
173. Vakonderwijs en Visscherijschool. – Ibid., p. 110–120.
174. Thonijnen in de Noordzee. – Ibid., p. 124–127.
175. Goede en slechte vischjaren. – Ibid., p. 136–138.
176. Het vergaan van de “Endeavour”. – Ibid., p. 138.
177. Carbolsmaak bij visschen. – Ibid., p. 172–174.
178. Ueber den gegenwärtigen Stand unserer Kenntnis von den Rassen der wichtigsten Nutzfische. – Rapp. Proc. Verb. Cons. Internat. Expl. de la Mer, **XXII**, 34 p.

1916

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180. De reorganisatie van den wetenschappelijken dienst ten behoeve der visscherijen. – Ibid., p. 54–56.
181. Plankton en Visscherij. (Openbare les bij de aanvaarding van het privaat-docentschap in de hydrobiologie en visscherijkunde aan de Amsterdamsche Universiteit op 10 October 1916). – Ibid., p. 75–98.
182. In memoriam BRUNO HOFER. – Ibid., p. 99–100.
183. De Noordzeevisscherij en de oorlog. – Ibid., p. 103–108.
184. Over "waterbloei"-vormende wieren en hun schadelijkheid voor de binnenvisscherij. – Ibid., p. 109–114.
185. Naturgeschichte der Sardelle. – Mitteil. D. Seefischerei-Vereins, No. 11/12, 6 p.

1917

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187. De Engelsche binnenvisscherij. – Ibid., p. 44–51.
188. De "Meerval" een drijvend laboratorium voor visscherijonderzoek. – Ibid., p. 72–81, 1 pl.

1918

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190. Bijdrage tot de kennis van de Noordzee-haringstammen. – Rapp. Verh., Rijksinst. Visscherijonderz., **I**, 4, 15 p., 1 bijlage, 9 tabellen.
191. Aanteekeningen over platvisschen. – Meded. Visscherij, **XXV**, p. 26–30.
192. Het zoetwaternannoplankton en zijn beteekenis voor de visscherij. – Ibid., p. 17–25, 38–43.

1919

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194. Bijdrage tot de kennis der inlandsche Zoetwater-Peridineeën. – Bijdr. Dierk., **XXI**, (Feestnummer dr. C. KERBERT), p. 123–134, fol.
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196. Overzicht der uitkomsten van onderzoekingen verricht in het belang der zoetwatervisscherij. – Ibid., Bijlage, p. 6–43, 1 pl.

1920

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1921

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203. Verslag omtrent onderzoekingen met fuiken in de Vecht bij Vreeland. – – Ibid., Bijlage B, p. 19–26.

1922

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205. Aanteekeningen over de Hydrografie. In: Flora en Fauna der Zuiderzee. Helder, p. 33–43.
206. Visschen: In: Idem, p. 426–442.
207. Mededeeling betreffende het voorkomen van *Leucaspius delineatus* Sieb. in Noordhollandsche en Utrechtsche polderwateren. – Tijdschr. Ned. Dierk. Ver., (2), **XVIII**, Verslagen, p. CXLVI.

1923

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209. Rapport omtrent onderzoekingen aangaande den groei van den Brasem in verschillende wateren. – Ibid., p. 221–253, 1 pl., 4°.

1924

210. Het plankton van het Heldersche Kanaal in 1916. – In: Versl. Gezondheidscomm. te Helder 1924, Bijlage IV, 20 p., 1 pl.

1925

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Dr H. C. REDEKE
29 Augustus 1873 – 10 April 1945

Op den 10en April 1945 is te Vreeland, waarheen hij in het voorjaar van 1944 was geëvacueerd met het oog op zijn gezondheid, Dr H. C. Redeke overleden. Hoewel hij geen oorlogsslachtoffer in directen zin genoemd kan worden, was zijn onverwacht heengaan toch een gevolg van de oorlogsomstandigheden, die voor hem, als diabeteslijder, bijzondere moeilijkheden met de voeding meebrachten en de door zijn ziekte toch reeds verzwakte gezondheid den laatsten slag gaven. In zijn retraite in Vreeland hield Dr Redeke zich tot het laatste toe bezig met de bewerking van zijn boek over de Hydrobiologie van Nederland, dat helaas door zijn plotseling heengaan niet geheel beëindigd kon worden. Gelukkig is het deel, dat het zoete water van Nederland behandelt, als manuscript gereed en dit kan door de goede zorgen van Mej. A. P. C. de Vos, die jarenlang zijn assistente en medewerkster is geweest, spoedig in druk verschijnen. Aldus is deze belangrijke samenvatting van Redeke's levenswerk voor ons behouden, hoewel het jammer is, dat het deel over het brakke water nog niet geschreven was. Het zou misschien mogelijk geweest zijn met behulp der losse, voorloopige aanteekeningen ook dit deel te schrijven, maar Mej. de Vos heeft gemeend hiervan te moeten afzien, omdat slechts de auteur in staat geweest zou zijn dit in den perfecten vorm te doen, dien wij van hem gewend waren en die zijn publicaties hun zoo groote waarde verleenen.

Het is niet noodig hier te herhalen wat reeds in 1943 door ons over hem geschreven werd, bij de herdenking van zijn zeventigsten verjaardag. De tekst daarvan kon toen alleen in proef aan den jubilaris worden aangeboden, door de oorlogsomstandigheden zag deze eerst korten tijd geleden in dit tijdschrift het licht. Dr J. Verwey heeft de verdiensten van den overledene herdacht in het Vakblad voor Biologen van Juli 1946, waarvan de overledene een der oprichters was. De Nederlandsche Dierkundige Vereeniging herdenkt in hem den voortreffelijken organisator, die zoo vele jaren haar Station en haar Bibliotheek van zijn goede zorgen deed profiteeren, de Visscherijen danken hem een lange reeks voortreffelijke publicaties en een schare jongere biologen zal hem blijven zien als den man aan wiens enthousiasme en toewijding zij hun belangstelling en liefde voor de Hydrobiologie te danken hebben.

H. Engel.